A baited remote underwater video survey of the Goukamma Marine Protected Area's ichthyofauna and a subsequent community structure comparison with the Betty's Bay, Stilbaai, and Tsitsikamma Marine Protected Areas

by

Jackson Willy Dando
DNDJAC001

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Supervisor: **Associate Professor Colin G. Attwood**
Department of Biological Sciences, University of Cape Town

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Name:	**Jackson Willy Dando**
Student Number:	**DNDJAC001**
Course:	**BIO5010W**

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Abstract

The Goukamma Marine Protected Area (GMPA) along the South African south coast has been in existence since 1990. The MPA encompasses 40.2 km^2 of subtidal ocean, 76% of which is made up of sandy substrata and the remainder of which is made of rocky reefs. The imbalance in protected habitat type ratios prompted a proposal for an extension of the MPA's seaward boundary, referred to as the new no-take zone (NNTZ), and a restructuring of its eastern boundary, referred to as the new exploited zone (NEZ). The proposed boundary changes would increase the amount of protected reef by 53% and the overall size of the MPA by 38%.

Goukamma has been surveyed using controlled angling surveys (CAS) and underwater visual census (UVC) but has yet to be surveyed using baited remote underwater video (BRUV). I collected and analysed mono-BRUV data over five years to determine patterns in fish community structure in Goukamma and compare it to the pre-existing CAS and UVC data. BRUVs are less invasive and more robust than the other two survey methods and have the potential to become the predominant method of surveying ichthyofaunal communities in South Africa. This work is therefore also intended as a baseline BRUV survey.

BRUVs were deployed in Goukamma from 2013 to 2017. The survey produced 328 successful deployment records between 5-41.5 m across reef and sand sites. Date, site coordinates, depth, habitat type, protection zone were used as variables to explain patterns in the fish community data. Fish abundances were recorded using the MaxN metric. MaxN counts were recorded at the instance when the highest number of individuals of each species were present in a single video frame. The deployment records were converted into a single data frame and analysed using the RStudio integrated design environment.

Ariids, scyliorhinids, serranids, sparids, and triakids were the most well represented ichthyofaunal families in Goukamma. *Boopsoidea inornata*, *Cheimerius nufar*, *Chrysoblephus laticeps*, *Galeichthys feliceps*, *Mustelus mustelus*, *Pachymetopon aeneum*, *Poroderma africanum*, *Poroderma pantherinum*, and *Spondyliosoma emarginatum* were the most frequently observed species throughout the MPA.

Habitat type was identified as the primary determinant of diversity and abundance in the GMPA using multifactor analysis of variance (ANOVA) tests (species richness: F = 191.155,

$P < 0.001$; relative abundance: $F = 96.111$, $P < 0.001$) and Wilcoxon signed rank tests (Shannon-Wiener: $W = 21\ 102$, $P < 0.001$; Simpson: $W = 18\ 553$, $P = 4.85 \times 10^{-10}$). The reef sites supported a higher species richness and abundance than sandy sites throughout the MPA (Tukey: $q = -4.41$, $P < 0.001$ and $q = -2.12$, $P < 0.001$, respectively). Diversity and abundance were correlated with each protection zone's predominant habitat type. Exploited zones had significantly higher diversity and abundance than protected zones as a result of the imbalance in Goukamma's protected habitat type ratio (species richness: $F = 27.740$, $P = 7.65 \times 10^{-16}$; abundance: $F = 10.438$, $P = 1.51 \times 10^{-6}$; Shannon-Wiener: $W = 17\ 314$, $P = 4.58 \times 10^{-6}$; Simpson: $W = 15\ 896$, $P = 3.42 \times 10^{-3}$). The NNTZ had significantly higher species richness and abundance than the NEZ (Tukey: $q = 3.07$, $P < 0.001$ and Tukey: $q = 1.48$, $P < 0.001$, respectively). The proposed changes will therefore substantially boost diversity and abundance of protected fishes in Goukamma.

BRUV samples in Goukamma recorded an overall higher species richness and abundance of sparids, chondrichthyans, and other reef-associated species than CAS and UVC samples. Over 90% more chondrichthyans were recorded in the BRUV samples than by the other two methods. BRUVs are therefore considered to be a suitable replacement for CAS and UVC surveys for the monitoring of South Africa's shallow subtidal ichthyofauna.

BRUV data from Betty's Bay, Stilbaai, and Tsitsikamma were available for comparison with the Goukamma data, allowing for an extensive analysis of the south coast's ichthyofaunal communities. A combined data frame of 466 successful BRUV deployments from the four study areas was created. Multi-factor ANOVA tests indicated that location ($F = 27.1$, $P = 1.00 \times 10^{3}$), depth zone ($F = 17.4$, $P = 1.00 \times 10^{3}$), protection status ($F = 23.1$, $P = 1.00 \times 10^{3}$), and habitat type ($F = 91.8$, $P = 1.00 \times 10^{3}$) were all significant in determining community structure among the study areas. Reef sites had higher species richness and abundance than sand sites and species richness and abundance decreased from east to west along the south coast according to subtropical subtraction. However, the presence of an additional habitat type in Betty's Bay, namely kelp forests, resulted in it having a higher species richness and abundance than Stilbaai to the east. Betty's Bay's community structure was the least similar to the other three study areas as a result of the localised kelp forests in and around the MPA. These kelp forests shifted Betty's Bay's community structure away from the sparid-dominance observed in Stilbaai, Goukamma, and Tsitsikamma and towards a carangid- and scyliorhinid-dominance.

However, cold-water associated sparids such as *Pterogymnus laniarius* were more abundant in Betty’s Bay than the other study areas.

Almost 80% of the species recorded among the study areas were represented in two or more of the four MPAs, indicating a good degree of redundancy of protection along the south coast within the depth ranges sampled. These data suggest that the Cape south coast is adequately protected from the perspective of fish representation. Review of the De Hoop, Sardinia Bay, and Bird Island MPAs should be conducted to further examine complementarity and redundancy of protection along South Africa’s south coast.

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Abbreviations

Abbreviation	Expansion
ABT	Aichi Biodiversity Target
AIC	Akaike information criterion
ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
BBMPA	Betty's Bay Marine Protected Area
BRUV	Baited remote underwater video
CAS	Controlled angling surveys
CAP	Canonical analysis of principle coordinates
CapeNature	Western Cape Nature Conservation Board
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CFM	Conventional fisheries management
COMPARE	Criteria and Objectives for Marine Protected Area Evaluation
CSV	Comma-separated values
CPUE	Catch per unit effort
DEA SA	Department of Environmental Affairs South Africa
deg.	Degrees
DI	Diversity index
DZ	Depth zone
EAF	Ecosystem approach to fisheries
EEZ	Economic exclusive zone
EZ	Exploited zone
FOV	Field of view
GLM	Generalised linear model
GMPA	Goukamma Marine Protected Area
i.e.	Id est
IUCN	International Union for Conservation of Nature
km	Kilometre
m	Metre
METT	Management Effectiveness Tracking Tool
NEZ	New exploited zone
nm	Nautical mile
NNTZ	New no-take zone
NRF	National Research Foundation
NTZ	No-take zone
PERMANOVA	Permutational multivariate analysis of variance
PISCO	Partnership for Interdisciplinary Studies of Coastal Oceans
SAEON	South African Environmental Observation Network
SAIAB	South African Institute for Aquatic Biodiversity
SANParks	South African National Parks
SMPA	Stilbaai Marine Protected Area
SOMSAMPA	State of Management of South African Marine Protected Areas
TMPA	Tsitsikamma Marine Protected Area
WWF	World Wide Fund for Nature
UK	United Kingdom
UNEP-WCMC	United Nations Environment World Conservation Monitoring Centre
USA	United States of America
UVC	Underwater visual census

Figures and tables

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CHAPTER 1: Introduction

1.1 Overfishing and the state of global marine resources

The world's oceans are at risk of collapse within our lifetimes. It is estimated that over 90% of all large marine fishes have already been consumed by humans (Graham, 2003), and that many marine mega-vertebrates are at risk of critical dispensation or functional extinction as a result of overexploitation (Jackson et al., 2001). The primary driver behind the devastation of our marine resources is overfishing, a phenomenon arising from historically unchecked increases in fishing pressure to meet the demands of an ever-growing human population (Quinn & Deriso, 1999).

Over 2.7 billion people actively rely on marine resources as their primary source of sustenance or income (The United Nations Ocean Conference, 2017), the cumulative impact of which is overwhelming global marine ecosystems (National Research Council, 2001; Feike, 2008). Current estimates suggest that the mean human consumption of fish per capita has risen above 20 kg per annum (FAO, 2016), equating to a total consumption in excess of 154 billion kg each year. This does not include marine mammals, reptiles, and shellfish, the consumption of which has more than doubled since the 1960s (Lackey, 2005).

Overfishing is a blanket term for a diverse group of phenomena which have been defined over the history of conventional fisheries management (CFM) based on different driving factors and management plans (Pauly, 1994; Froese, 2004; Beamish et al., 2006). It can broadly be defined as the overexploitation of a marine resource to the point where it cannot effectively regenerate through natural reproduction. The two primary and most widely recognised forms of overfishing are growth and recruitment (Parrish, 1999).

Growth overfishing occurs when a population of marine organisms are harvested at an average size below that which would produce the maximum reproductive yield per recruit (Beverton & Holt, 1957; Pauly, 1994). Recruitment overfishing occurs when the spawning biomass of a population becomes depleted to the point where there are not enough fecund organisms to effectively reproduce and recruitment declines proportionally with adult abundance (Pauly, 1994; Allen et al., 2013). Further definitions of overfishing focus on combining or expanding upon these two core phenomena (Pauly, 1994), and include biological (Clark, 2006), convenience (Froese, 2004), economic (Temming & Temming, 1992), ecosystem (Botsford et al., 1997), genetic (Palero et al., 2011), longevity (Beamish et al., 2006), Malthusian (Pauly, 1990), and serial overfishing (Soh et al., 2001).

The implications of overfishing extend far beyond that of just depleting targeted fish stocks, as negatively affected predator populations with low reproductive rates such as birds, chondrichthyans, and marine mammals may require decades to recover (Dayton et al., 1995). Disruptions to the balance of marine ecosystems through the targeted removal of integral species can have detrimental effects on the structure and diversity of entire benthic communities (Jennings & Kaiser, 1998). A further deleterious side-effect of overfishing is that of increased mortality in commercially undesirable bycatch species due to non-selective fishing gear (Roberts, 1997), which is subsidised by the high value of target species (Botsford et al., 1997).

Traditionally, fisheries managers have attempted to combat overfishing through the use of CFM, the primary goal of which is to sustainably protect our marine resources whilst simultaneously extracting the maximum possible social and economic benefits from them (Lackey, 2005). An issue with CFM is that the relationships between a target population's productivity and other components of the ecosystem are often overlooked or ignored (Attwood et al., 2000). Alternative, more holistic approaches to fisheries management are the ecosystem approach to fisheries (EAF) and marine spatial planning (MSP).

The EAF differs from CFM in that it focuses on area-based management of habitats and ecosystem integrity as opposed to vertically integrated, sector-based management of the target resource (Garcia et al., 2003). This form of management shifts from protecting only the target species to including as much of the surrounding ecosystem and biodiversity as possible (Dayton et al., 1995). MSP involves coordinating the sustainable use of marine resources through the inclusion and cooperation of all affected parties, including commercial industry, conservationists, the government, and recreational users (Douvere, 2008). Spatial management plans have been a longstanding method of CFM, but it is only in recent years that the use of marine protected areas (MPAs) has begun to be utilised to transition from CFM to forms of EAF and/or MSP management (Sainsbury & Sumaila, 2003; Crowder & Norse, 2008; Harmelin-Vivien et al., 2008).

1.2 Marine protected areas

MPAs are spatially-demarcated bodies of water with restrictions placed upon them to promote the effective conservation and management of marine biodiversity and reduce conflict between diverse resource users (Edgar et al., 2007; Cole et al., 2009). Soulé and Simberloff (1986) divide the purpose of reserves, and in this context MPAs, into three aims: to preserve species of interest, to maintain biodiversity, and to preserve biological communities. The specific objectives of individual MPAs may differ from area to area for a variety of reasons, but their over-arching goal is to provide refuge for populations of target and nontarget bycatch species, as well as to allow habitats affected by anthropogenic perturbances to recover and regenerate such that they may continue to be sustainably utilised by future generations (Gell & Roberts, 2003).

Most MPAs are located within countries' territorial waters (Spalding et al., 2013), as the international law of the sea defined by the United Nations Convention on the Law of the Sea diminishes the authority of individual governments over the high seas. As such, there is a much higher level of protection in national waters (18.45%) than in international waters (1.18%). However, these values are skewed by the fact that national waters comprise only 39% of the global ocean, whilst international waters make up 61% (UNEP-WCMC & IUCN, 2020). A more accurate representation is that national MPAs protect 7.19% of the global ocean whilst international MPAs protect 0.72%, equating to a total of 7.91% (Figure 1).

As of January 2020, 16 928 registered MPAs were in place around the globe covering approximately 28.66 million km^2 of the world's oceans (UNEP-WCMC & IUCN, 2020). Over 70% of the area protected by MPAs is located in the national waters and/or territories of Australia, the Cook Islands, France, Mexico, New Zealand, the United Kingdom (UK), and the United States of America (USA).

No management system is without its flaws, and the concept of closed fishing areas in MPAs has often come under fire from commercial fisheries and local stakeholders for creating short-term issues that outweigh proposed long-term benefits (Agardy et al., 2003; Jones, 2008). Management of MPAs differs vastly between and even within countries, and can range from strictly-policed no-take zones to seasonally open zones, or even "paper parks" with minimal to no enforcement (Garcia et al., 2003). One of the primary concerns relating to no-take zones in

MPAs is that they displace fishing effort to the surrounding areas and exacerbate the rate of their depletion, as well as decreasing the catch per unit effort (CPUE) of fishermen targeting less mobile species (Bohnsack, 2000). Many of the shortcomings of MPAs arise from poor design, implementation, or management, in that their objectives and potential benefits are often poorly articulated to stakeholders, they are too small or ineffectively zoned and only create the illusion of protection, or they do more harm than good through the displacement of exploitation (Jones, 2001, 2009; Agardy et al., 2011). Despite these concerns, studies have found that MPA implementation often has a positive impact on surrounding fishing communities (Bohnsack, 2000; Fernandes et al., 2005; Mascia et al., 2010; Grüss et al., 2011).

MPAs are by no means toted as a panacea (Sink, 2016): no level of anthropogenic management or intervention can ever control the turbulent nature of our oceans. External factors beyond overfishing such as climate change, El Niño-Southern Oscillation, ocean acidification, and plastic pollution are all serious threats to populations residing inside MPAs (Hoegh-Guldberg & Bruno, 2010). For the greatest chance at success, the areas surrounding MPAs need to be managed in as sustainable a manner as possible (Agardy et al., 2011), so as to mitigate the chances of extrinsic perturbances negating the effects of their protection (Allison et al., 1998; Johansen et al., 2011). Sustainable management is however often not the prevailing scenario (Costello et al., 2016), especially in the case of older MPAs, where establishment either went ahead without suitable articulation of the intended objectives or design parameters were constrained by socio-political pressure (Götz, 2005).

MPA networks exist as a method for co-operating governments or judiciaries to establish groups of synergistic reserves at various spatial and protection levels to achieve objectives that individual MPAs cannot (PISCO, 2002; Chircop et al., 2010; McCook et al., 2010). These networks are generally considered as an improvement over individual MPAs when it comes to protecting against threats that extend beyond fishery related stressors (Fernandes et al., 2005; Clifton, 2009; Keller et al., 2009).

MPAs around the world

The first large-scale plan to establish an MPA in international waters was launched in December 2017 and saw 24 countries come together and agree to form the Ross Sea Region MPA in Antarctica (CCAMLR, 2017). It currently encompasses over 2% of the Southern Ocean and is the largest protected area in existence (2.06 million km^2), followed closely by the Marae Moana, which constitutes the entire economic exclusive zone (EEZ) of the Cook Islands (1.98 million km^2) (Christie et al., 2017; Taylor, 2017; UNEP-WCMC & IUCN, 2020).

Other notably large MPAs around the world include the Papahānaumokuākea Marine National Monument (1.5 million km^2, USA), the Pacific Remote Islands Marine National Monument (1.25 million km^2, USA), the South Georgia & the South Sandwich Islands MPA (1 million km^2, UK), the Le Parc Naturel de la Mer de Corail National Park (1.3 million km^2, France), the Palau National Marine Sanctuary (500 000 km^2, Palau), and the Pitcairn Islands Marine Reserve (840 000 km^2, UK) (Spalding et al., 2013; Christie et al., 2017; UNEP-WCMC & IUCN, 2020).

Whilst the establishment of these large-scale MPAs is a positive step towards achieving more synergistic and inclusive MPA networks, there are concerns that their size might actually be counterproductive in that their contribution to Aichi Biodiversity Target (ABT) 11 will not be as effective as splitting the same area coverage between smaller, more manageable MPAs (De Santo, 2013; Thomas et al., 2014; Devillers et al., 2015; Jones & De Santo, 2016). There are valid arguments for both small MPAs, which are easy to manage and monitor, and large MPAs, which are more inclusive of different habitat types and mobile species (Pala, 2013; Toonen et al., 2013). It is important that a balance is found between the different sizes and management styles of MPAs to best utilise their respective strengths and weaknesses when working towards most effectively fulfilling ABT 11 (Thomas et al., 2014).

An argument against the use of large MPAs as an effective tool for fisheries management is that the size of the MPA required to adequately protect organisms needs to be at least half of the productive habitat, which would require a financially unviable increase in total fishing effort in exploitable areas and result in economic overfishing (Pauly, 1994; Parrish, 1999). Extended overexploitation of open areas can eventually result in a diminishing percentage of the exploitable population being available to fisheries, and prior studies highlight historical fishing effort and trawling rate increases of up to 244% and 429% in similar scenarios (Parrish, 1999; He et al., 2007). Damage to the exploited part of the ecosystem by pressure increases of this magnitude would likely be considerable and potentially irreparable. There are also concerns that the implementation of large MPAs and the subsequent reduction of the age structure of target species in surrounding waters would lead to decreased annual landings and highly variable recruitment in affected species.

A 1999 study on the viability of MPAs as a fisheries management tool concluded that the socio-economic and environmental issues associated with establishing large MPAs could be mitigated and better managed through the use of CFM, such as seasonally restricted fishing zones and the tactical closing of nursery areas (Parrish, 1999). However, the study placed emphasis on highly mobile, diadromous, and/or migratory species, which served to produce a bias in the reported size of MPAs required for adequate protection (Lackey, 2005).

Parrish's (1999) argument that a minimum of 50% of an area's productive habitat is required for effective MPA implementation falls short when scrutinised. A comparison of the managed and unmanaged sides of Kenya's Mombasa MPA showed an increased yield of up to 50% by fishermen operating in waters adjacent to the managed side (McClanahan & Manga, 2000). Data were collected over the course of seven years using pre-existing fishery statistics and baited traps. Even after the size of the MPA was halved the resultant CPUE was only reduced by 30%, demonstrating the potential for MPAs to sustain abundant communities disproportionate to their size. The results of the study suggest that tropical fisheries that close a mere 10-15% of their operational area would benefit more from the subsequent regeneration and spillover of resources than if they were to exploit the total area available to them.

This is not to say that all fisheries around the world would be improved by cordoning off 15% of their exploitable areas, but rather that the application of diverse operational strategies, tailored to each individual MPA based on preliminary research, plays a critical role in effective and ethical MPA implementation and management (Gubbay, 1995; Rodrigues et al., 2004). If MPAs are implemented without sufficient individual evaluation and monitoring they stand the chance of alienating local stakeholders, failing to fulfil expectations, and lowering the credibility of MPAs as a tool for conservation and fisheries management in the future (Mosquera et al., 2000; Hilborn et al., 2004; Hansen, 2013).

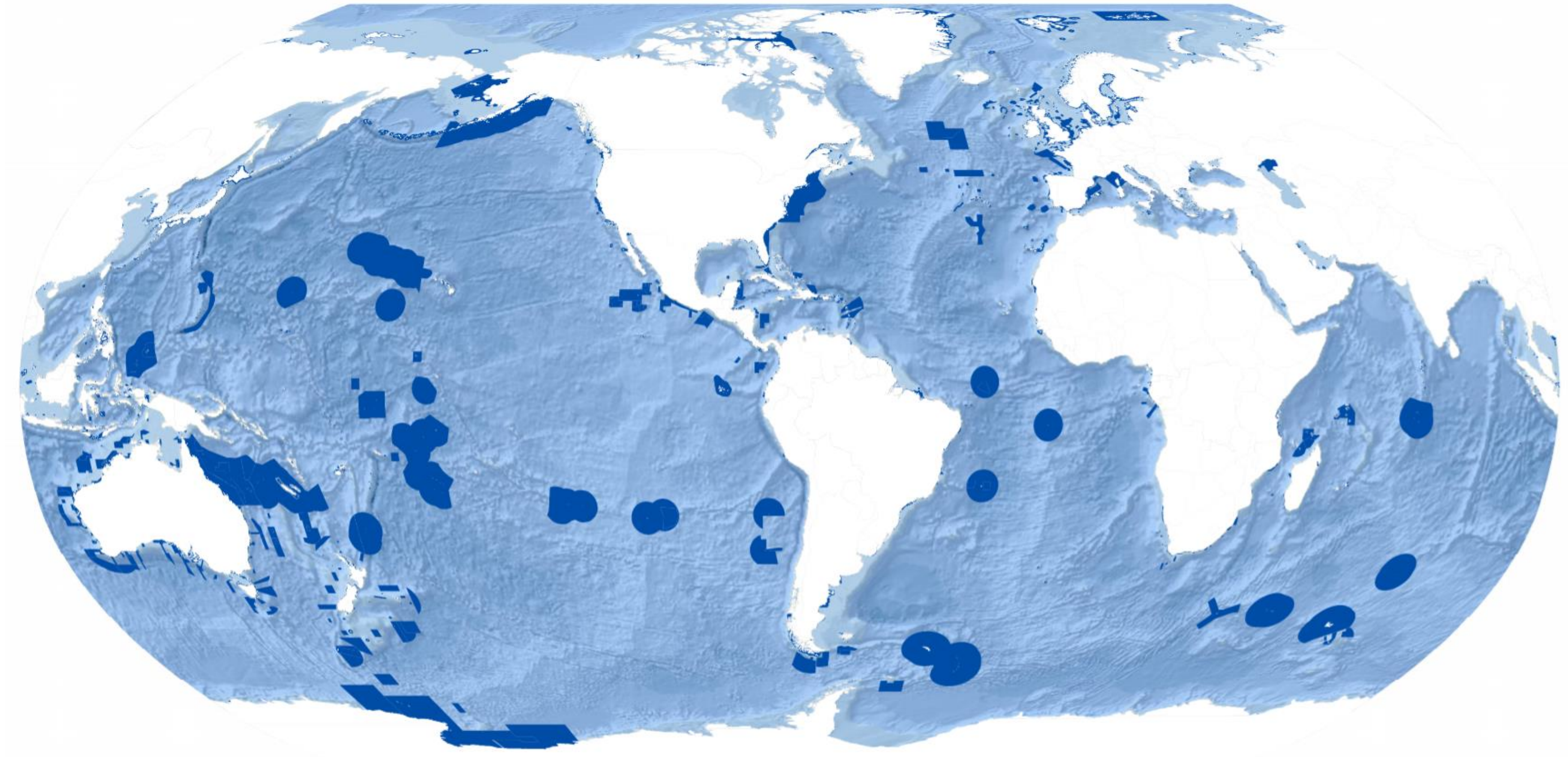

Figure 1: Distribution of MPAs around the globe: 7.91% of the global ocean is covered by protected areas, of which 2.46% are no-take zones. Adapted from *Protected Planet: The World Database on Protected Areas* (UNEP-WCMC & IUCN, 2020).

1.3. South Africa's coastal environment and MPA distribution

1.3.1 The coastal environment

South Africa's coastline stretches approximately 3 190 km from the Namibian border on the west coast, around the southern-most tip of the continent at Cape Agulhas, and up to the Mozambican border on the east coast (Tinley, 1985; Nichols, 2015). It plays host to a unique interaction between two major ocean systems: the Atlantic Ocean along the west coast and the Indian Ocean along the east coast.

The west coast is dominated by the cold, equatorward Benguela Current and the east coast is dominated by the warm, poleward Agulhas Current. The mixing of these cool-temperate and subtropical environments results in a warm-temperate environment along the south coast (van der Elst, 2007; Griffiths et al., 2010; Spencer et al., 2016). The subtropical east coast can further be divided into a northern and a southern section (van der Elst, 2007).

South Africa exercises jurisdiction over 1 535 538 km^2 of ocean, which is split amongst the territorial waters, contiguous zones, and EEZs of the mainland and Prince Edward Islands territory (1 068 659 km^2 and 466 879 km^2 respectively) (The University of British Columbia, 2016). Of the country's marine jurisdiction, 15% is currently protected by MPAs. This is however skewed by the 180 000 km^2 offshore Prince Edward Islands MPA. Only 5.4% of the country's national jurisdiction is protected by MPAs, which falls short of achieving ABT 11 (Griffiths et al., 2010; Marine Conservation Institute, 2018). Despite the low level of overall national protection, over a fifth of South Africa's coastal zone is protected by MPAs (Table 1) (Griffiths et al., 2010; Sowman et al., 2011; Sink et al., 2012; DEA SA, 2016).

Over 12 900 species of marine animals have been recorded in South Africa's EEZ, of which roughly 33% are endemic (van der Elst, 2007; Griffiths et al., 2010). At least 2 200 of these species are fishes (Solano-Fernández et al., 2012). This is equivalent to almost 7% of the total number of known marine fish species worldwide, and an impressive 13% of represented families are endemic to our waters, the highest proportion of which have been recorded along the south coast around Port Elizabeth (Turpie et al., 2000; van der Elst, 2007). Species richness is highest in the subtropical north-east closest to Mozambique and decreases southwards towards the warm- and cool-temperate zones off the Eastern and Western Cape provinces, respectively, due to the effects of subtropical subtraction (Turpie et al., 2000). The coastline also harbours over 290 functional estuaries (DEA SA, 2016), with a total estuarine area of roughly 900 km^2, although nearly half of this is made up by the St. Lucia Lake system in the KwaZulu-Natal province (Driver et al., 2012).

A 2007 analysis of the distribution of marine fishes along the coastline indicated that protecting strategic sections amounting to only 650 km could effectively conserve all inshore fish species (van der Elst, 2007), however, this is assuming that these protected sections are effectively managed and that the fish populations are self-sustaining. Sufficient research has not been conducted into determining the efficacy of South Africa's MPAs (Chadwick et al., 2014), although there are suggestions that they fall short of representing the full diversity of our complex ocean system (Griffiths et al., 2010). South Africa's coastline can be subdivided into 136 different coastal and marine habitats (Harris et al., 2014).

The *2016 South Africa Environment Outlook Report* indicated that 7.4% of the country's marine resources are under-exploited, 48.1% are optimally-exploited, 14.8% are over-exploited, and the status of the remaining 29.6% requires further review (DEA SA, 2016). A more indicative view of the state of South Africa's marine resources can be seen in the condition of our commercially important linefish species, of which 68% have experienced population collapse, 11% are over-exploited, and only 16% are optimally-exploited (WWF, 2011; DEA SA, 2016).

There are currently 22 recognised commercial fisheries operating in South African waters (Griffiths et al., 2010). Commercial harvest methods include linefishing, longlining, purse-seine netting, trapping, and trawling (WWF, 2011). The *2000 South African Marine Biodiversity Status Report* highlighted the fact that South African marine environments were showing symptoms of overexploitation and degradation over 19 years ago (Attwood et al., 2000). The report listed potential threats to our biodiversity as aquaculture and specimen collection, changes to the benthos, climate change, commercial and recreational overfishing, development of the coastal zone, invasion of alien species, mining and pollution, and unsustainable bycatch of commercially undesirable species.

1.3.2 South African MPAs

South Africa has the third longest coastline in Africa and plays host to a wide variety of coastal and offshore environments and a resultingly high level of ichthyofaunal endemics, which we have a responsibility to conserve. Following the implementation of Operation Phakisa's marine protection initiative in 2019, the country now has 42 coastal and offshore MPAs (Figure 2), amounting to a total protected area of 58 255.6 km^2. Prior to this, only 23 gazetted MPAs existed along South Africa's coastline, which equated to less than 0.5% of the country's EEZ. A further 48 610.3 km^2 of marine habitat needs to be protected in order to fulfil ABT 11.

Table 1: MPAs under South Africa's national jurisdiction prior to Operation Phakisa, amounting to a total protected area of 4 455.6 km^2. The Prince Edwards Island territory is not included (Tunley, 2009; Chadwick et al., 2014; Visagie & Saul, 2014; Spencer et al., 2016; Marine Conservation Institute, 2018; UNEP-WCMC & IUCN, 2020).

MPA	Size (km^2)	Year established	Management agency
Eastern Cape			
Amathole	247.8	2011	ECPTA
Bird Island Group	70.4	2004	SANParks
Dwesa-Cwebe	193	1989	ECPTA
Hluleka	44	2000	ECPTA
Pondoland	1 238.2	2004	ECPTA
Sardinia Bay	12.9	2000	Nelson Mandela Metro
Tsitsikamma	186	1964	SANParks
KwaZulu-Natal			
Aliwal Shoal	126	2004	EKZNW
iSimangaliso	443	1998	iSimangaliso Wetland Park Authority
Trafalgar	193	1979	EKZNW
Western Cape			
Betty's Bay	20.1	1981	CapeNature
De Hoop	288.9	1985	CapeNature
Goukamma	40.2	1990	CapeNature
Helderberg	24.6	1991	City of Cape Town
Robberg	42	1998	CapeNature
Rocherpan	1.5	1988	CapeNature
Stilbaai	20	2008	CapeNature
Table Mountain National Park	984	2004	SANParks
West Coast National Park	280	1985	SANParks

The Amathole MPA is made up of three separate sections, Gxulu, Gonubie, and Kei, each of which used to be an individual MPA established in the 1980s. iSimangaliso is the amalgamation of two former MPAs, Maputaland and St. Lucia, which were established in 1986 and 1979 respectively. The West Coast National Park is a suite of five MPAs, including Langebaan Lagoon, Sixteen-mile Beach, and Jutten, Malgas, and Marcus islands.

Operation Phakisa

The Phakisa Oceans Operation was initiated by the Presidency of South Africa in 2014 with the aim of fast-tracking the process of increasing the economic potential of the country's coastline and oceans (Harris et al., 2014). The concept was based on the Malaysian government's "big fast results" programme (Nichols, 2015). One of the primary intended outcomes of Operation Phakisa was to develop a representative MPA network to contribute to the sustainable management and exploitation of the country's marine resources and to fast track its progression towards accomplishing ABT 11. To this end, 21 new MPAs and expansions were proposed to reduce the number of unprotected habitat types by 85% and further increase the level of protection of already represented habitats (Harris et al., 2014). As of May 2019, 20 MPAs have officially been gazetted (Figure 2 and Table 2) (Mann, 2018; DEA SA, 2019a), raising South Africa's current national marine protection level from 0.4% to 5.4% (over 54 000 km^2) (DEA SA, 2019b).

Table 2: MPAs and expansions implemented through Operation Phakisa, amounting to an additional protected area of 53 800 km^2 (DEA SA, 2019a; Sink et al., 2019). Individual MPA gazette references can be found in Appendix 1.

MPA	Size (km^2)	MPA	Size (km^2)
Addo Elephant National Park	1 100	iSimangaliso (expansion)	10 700
Agulhas Bank Complex	4 300	Namaqua Fossil Forest	500
Agulhas Front	6 200	Namaqua National Park	550
Agulhas Muds	200	Orange Shelf Edge	1 800
Aliwal Shoal (expansion)	670	Port Elizabeth Corals	270
Amathole Offshore (expansion)	4 200	Protea Banks	1 200
Benguela Muds	90	Robben Island	600
Browns Bank Corals	340	Southeast Atlantic Seamounts	7 700
Cape Canyon	580	Southwest Indian Seamount	7 500
Childs Bank	1 200	uThukela Banks	4 100

The Prince Edward Islands (an offshore South African territory)

The Prince Edward Islands territory lies approximately 1 769 km south-east of Port Elizabeth and falls under South Africa's jurisdiction. It consists of two islands: Marion and Prince Edward. The MPA was established in 2013 and is managed by the South African Department of Environmental Affairs (DEA SA). There is a 22.2 km^2 no-take zone around each of the two islands as well as four sanctuary zones where fishing is prohibited that encompass a total area of 4 440.57 km^2. The remainder of the MPA is a controlled fishing zone which prohibits bottom-trawling and gill-nets. A cumulative protected area of over 180 000 km^2 makes the Prince Edward Islands MPA South Africa's largest MPA (Spalding et al., 2013).

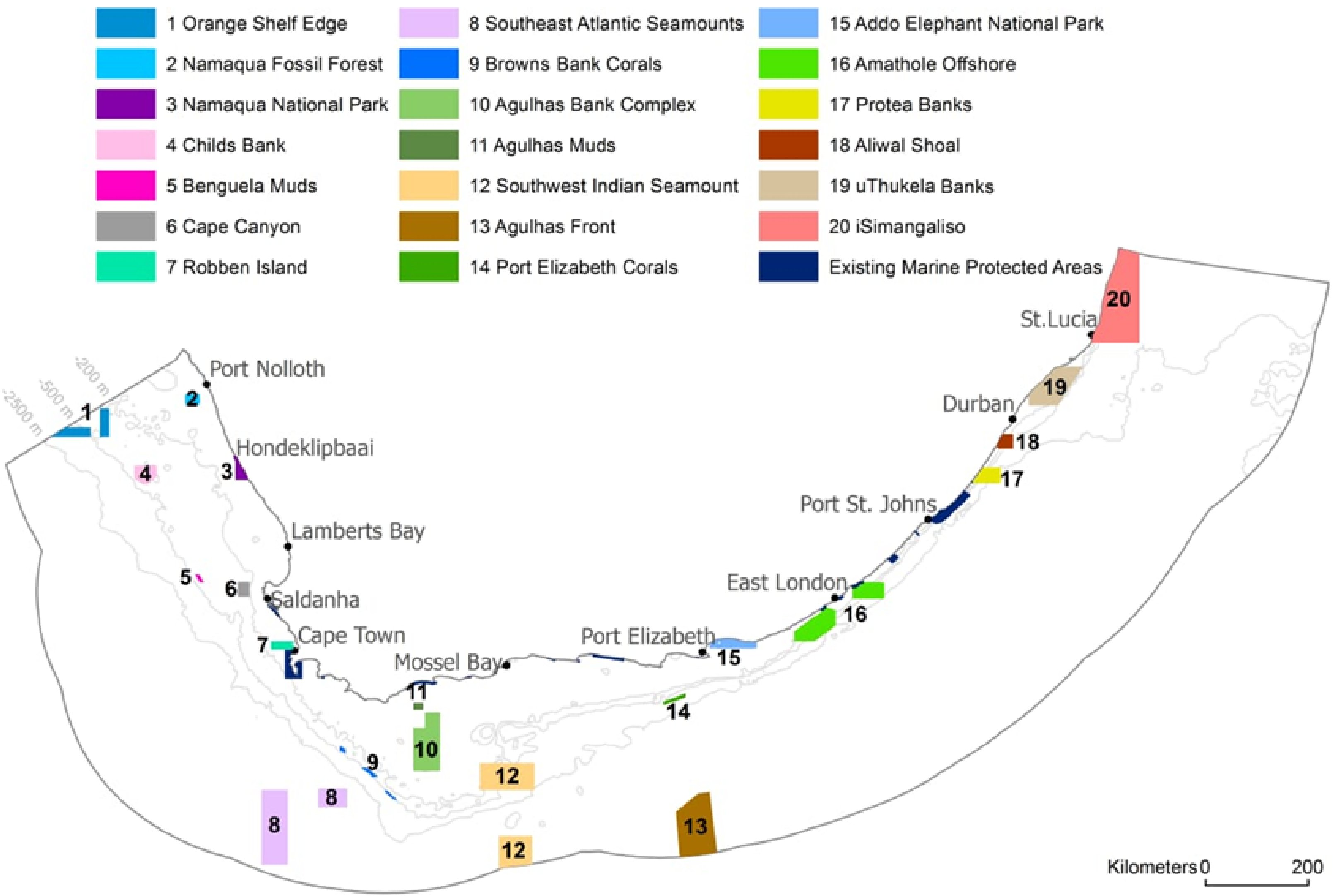

Figure 2: Distribution of MPAs in South Africa's EEZ after the implementation of Operation Phakisa. Adapted from the *South African Association for Marine Biological Research* (Mann, 2018; Sink et al., 2019).

1.4 Challenges associated with designing and evaluating MPAs in South Africa

Conflicts between marine resource users and MPA management have existed in South Africa since the Fish Protection Act was first passed in 1890, as a result of a lack of understanding of the human dimensions of fishery systems (Sowman et al., 2011). It is important that MPAs are designed and managed as optimally as possible such that they retain relevance in the country's volatile socio-political climate.

Tailoring MPAs to their individual socio-economic environments is a challenge enough in itself, but is further compounded by the fact that the vast majority of literature published on emerging trends and recommendations in MPA design stems from well-developed nations like Australia, Europe, and the USA. Whilst this hasn't always contextually suited the needs of developing nations (Ban et al., 2011), considerable progress has been made in these areas in the last decade (Christie et al., 2017; Madrigal-Ballestero et al., 2017; Trainer et al., 2017), rendering the literature more applicable. A more human-centred approach to management, wherein local stakeholders are not only consulted but actively involved in management and enforcement of policies is necessary in countries like South Africa where subsistence fishing is the primary source of sustenance for over 28 000 households (Clark et al., 2002; Sowman, 2006; Sowman et al., 2011; Horigue et al., 2012). A good example of this form of management can be seen in KwaZulu-Natal, where voluntary compliance with regulations has been observed in MPAs where local stakeholders have been involved in the decision-making process and boundaries are effectively structured (Napier et al., 2005; Chircop et al., 2010). The level of community compliance with regulations has been observed to drop in areas where subsistence needs are higher and issues of land ownership exist (Hauck & Sweijd, 1999; Chircop et al., 2010).

The boundaries of MPAs have historically not been as well designed as they could be, mostly due to the fact that they were largely designed based off of terrestrial models rather than bathymetric and ichthyofaunal pilot studies (Sowman et al., 2011). In many of these cases they were designed to coincide with the boundaries of coastal reserves to take advantage of pre-existing infrastructure, which whilst logical in the sense that implementation costs were reduced, did not account for areas' bathymetric profiles nor the distribution of their benthic substrata. Modern MPA design has shifted towards conducting preliminary ecoregional assessments such that bathymetric priorities are identified and accounted for when structuring MPA boundaries and protection zones (Hockey & Branch, 1997; Green et al., 2009). It is important that all affected stakeholders be involved from the inception of an MPA and its proposed boundaries, such that impasses between different sectors can be identified early and effectively dealt with before irreconcilable conflicts arise (Helvey, 2004).

As complex as appeasing local fishing communities can be, an even more challenging task often lies in reaching consensus between conservationists and commercial industrial interests. There is always an inherent trade-off associated with balancing conservation and fisheries outputs when considering no-take zones in MPAs. Research has shown that this trade-off can be reduced by implementing MPA networks, which can result in potentially smaller no-take zones spread across multiple, complimentary MPAs (Gaines et al., 2010). This solution suits both conservationists and fisheries management as the size reduction in individual no-take zones will result in larger exploitable areas for fisheries, and a network of interdependent MPAs will serve to protect a wider, more mobile array of species.

Whilst the conservation potential of future MPAs is an attractive concept, it is arguably more important that pre-existing MPAs are duly maintained and optimised . Some of these MPAs have been in place for decades, and adjustments to their infrastructure based on enhanced knowledge of their individual environments could prove as effective as creating entirely new MPAs. Methods for monitoring the efficacy of MPAs differ based on several factors, including the objectives of the specific study, the equipment and staff available on site, the bathymetric profile of the area being surveyed, and the type of species being monitored. Monitoring methods such as COMPARE (Hockey & Branch, 1997) and the METT III (Adams, 2018) are used to monitor MPAs as a whole, taking into account available budget, conservation goals, enforcement of regulations, infrastructure, management, and staffing. These methods are important in being able to determine if an MPA is performing sub-optimally, such that its management scheme can be accordingly adjusted. They also serve as valuable tools for highlighting where MPAs are excelling, not only for research purposes but as a medium for more transparent communication of MPAs' benefits with stakeholders and the public.

Signs that an MPA is functioning optimally and achieving its conservation goals include high species diversity and abundance with a varied representation of families, size structures inclusive of both the upper and lower end of organismal development (large fecund individuals as well as juveniles), measurable spillover into exploitable zones, and complementarity of adjacent and/or nearby MPAs. Redundancy of protection among MPAs is as important as complementarity, as it provides a safety net against climate change, especially for smaller MPAs, which are at greater risk of being adversely affected by external perturbances. Redundancy differs from complementarity in that redundant MPAs harbour members of the same species, acting as a safety net should one MPA become compromised, whereas complementary MPAs harbour different species, thus synergistically increasing the overall number of protected species. Redundancy and complementarity are not mutually exclusive, in most cases synergistic MPAs will complement one another by harbouring residential or less mobile c Surveys are required to monitor these factors. The three most common methods of surveying fish in coastal waters are baited remote underwater video (BRUV), controlled angling surveys (CAS), and underwater visual census (UVC).

Studying an MPA's ichthyofauna provides a good indication of the ecosystem's health as whole. High levels of chondrichthyans and other top predators indicate that an ecosystem is functioning healthily (Litzow & Ciannelli, 2007; Shin & Shannon, 2010). Fish are of high commercial and subsistence value (Lamberth & Joubert, 2014), and the conservation goals of MPAs more often than not include conserving fish populations such that they can recover from the effects of anthropogenic stressors. BRUV, CAS, and UVC have all extensively been used to monitor fish populations around the world. BRUV has been the least utilised of the three methods in South Africa and have only started gaining traction as a prominent benthic survey method in recent years. It is likely that BRUV will partially replace the earlier survey methods in future.

1.5 Baited remote underwater video systems

BRUVs are versatile, cost-effective sampling apparatus that allow scientists to remotely record the species composition and abundance of marine organisms at a chosen site with minimal negative impact on the benthos (Brooks et al., 2011; Dorman et al., 2012; Harvey et al., 2013; Schmid et al., 2017). There are numerous types of BRUV designs (Cappo et al., 2006; Heagney et al., 2007; Bouchet et al., 2018), the most basic of which consists of a camera with a bait cannister fixed in its field of view (FOV). A more sophisticated BRUV design is that of the stereo-BRUV, which was developed in Australia in the 1980s and makes use of two cameras mounted in such a way that they provide stereo-vision of the FOV (Cappo et al., 2006; Halse, 2013; Bernard et al., 2014). This allows for the accurate estimation of the size of organisms passing in front of the cameras.

BRUV is preferable to CAS and UVC methods in that it eliminates the inherent biases of the various angling techniques, can go deeper and stay underwater longer than scuba divers, and produces less variance in species diversity and abundance estimates (Brock, 1982; Cappo et al., 2001; Watson et al., 2010; Halse, 2013; Harvey et al., 2013). The use of BRUVs is non-extractive and does not pose the risk of inflicting physical harm or barometric trauma on the study organisms, and is thus one of the least impactful survey techniques available to marine scientists (Harvey et al., 2013; Bernard et al., 2014; Miller et al., 2017). BRUV is also advantageous in that it provides a permanent video record of each survey.

However, BRUVs are not without their limitations and cannot be safely deployed in the surf zone shallower than 5 m without running the risk of capsizing the deployment vessel during rig retrievals (Roberson et al., 2015). Substantial research has gone into exploring bait-related biases and methods to reduce the length of time required to process the video footage (Dorman et al., 2012; Wraith et al., 2013; Schmid et al., 2017). Studies have found a significant increase in the number of fish sampled when using baited rigs as opposed to un-baited rigs (Bernard & Götz, 2012; Hardinge et al., 2013), and that oily bait such as sardines yield the most consistent outcomes and thus tend to be the standardised bait types used in BRUV surveys (Dorman et al., 2012; Wraith et al., 2013; De Vos et al., 2014). Researchers from the University of Melbourne recommend that BRUV surveys be coupled with UVC where possible to reduce benthic diversity biases (Colton & Swearer, 2010).

The low impact and non-extractive nature of BRUVs makes them an ideal monitoring tool for MPA assessment (Hill et al., 2014). As such, BRUV has been used widely throughout the world to monitor community structure and diversity in MPAs and other areas of ecological interest (see Appendix 2 for a list of global references).

BRUV surveys in South Africa

South Africa's deep water habitats have long been out of reach of researchers due to the high costs associated with sampling them (Griffiths et al., 2010), but the advent of more pressure-resistant camera housings has opened the gateway for the exploration and assessment of fisheries' impacts on South Africa's deep, offshore reefs through the use of BRUV (Bernard et al., 2014). They have been used for numerous purposes along the South African coastline, including estuarine community evaluations, fishery impacts and stock assessments, and the monitoring of MPA efficacy. The robust nature of their design and unsophisticated deployment technique make them ideal for use in rough terrain and areas where trained personnel are limited.

BRUV has already been used to examine the community structure in and around several MPAs along the south coast, including Betty's Bay (Roberson et al., 2015, 2017), Bird Island (Heyns-Veale et al., 2019), De Hoop (Heyns-Veale et al., 2019), Goukamma, Stilbaai (De Vos et al., 2014), and Tsitsikamma (Bernard & Götz, 2012; Halse, 2013; Bernard et al., 2014; Heyns-Veale et al., 2016, 2019; Parker et al., 2016a,b), as well as the East Kleinemonde Estuary, an ecologically and economically important estuarine habitat in the Eastern Cape (Turpie et al., 2009; Becker et al., 2010). BRUV has also been utilised in Algoa Bay (Chalmers, 2012), False Bay (Sanguinetti, 2013; Carr, 2014; De Vos et al., 2015), and the Amathole, iSimangaliso, and Pondoland MPAs (Dames et al., 2020; Heyns-Veale et al., 2019) to monitor the community structures of reef fishes in and out of protection zones.

The south coast is the centre of the distribution range for many of South Africa's endemic marine fishes and has a long history of fishing (Griffiths, 2000; Clark et al., 2002), which places an added importance on the maintenance and optimisation of the region's MPAs. The Goukamma Marine Protected Area (GMPA) is located in the centre of the south coast and has yet to be surveyed with BRUV. There has been a proposal for the restructuring of the MPA's boundaries in the pipeline for over ten years (Götz et al., 2009a), which presents a good opportunity to use BRUV to evaluate the proposed changes. BRUV could play a pivotal role in producing the necessary evidence to validate the proposal and expedite its implementation. Goukamma's central positioning also provides an opportunity to test the effects of subtropical subtraction along the south coast, whereby areas to east and west of the MPA should have a higher and lower species richness and abundance respectively (Turpie et al., 2000).

1.6 Goukamma Nature Reserve and MPA

The Goukamma Nature Reserve was originally established in 1974 and was proclaimed a Provincial Nature Reserve in 1994 (Spencer et al., 2016). The reserve falls within the Cape Floristic Region (Manning & Goldblatt, 2012). It covers an area of 26.79 km^2 and contains a natural semi open-closed estuary, which is fed by the Goukamma and Homtini rivers and reported to be one of the only natural-condition estuaries left along South Africa's coastline (i.e. artificial breaching is seldom carried out) (Spencer et al., 2016). It is important that this estuary be maintained as many of the other regional estuaries have collapsed due to climate change, drought, habitat degradation, overexploitation, and pollution (Whitfield & Cowley, 2010), which may have compromised the south coast's viability as a nursery for juvenile fish. Goukamma's coastline forms part of a dune formation known as the Wilderness Dune Cordons (Götz, 2005), which run parallel to the ocean and reach widths in excess of 300 m (Tinley, 1985; Illenberger, 1996).

The GMPA was established adjacent to the nature reserve in 1990 with the objective of conserving important offshore reef habitats and the commercially important species that inhabit them (Götz, 2005; Mann et al., 2014a). It extends 16.4 km eastwards from Buffalo Bay towards the town of Sedgefield and 1.852 km (1 nm) out to sea, encompassing 40.2 km^2 of subtidal ocean (Götz et al., 2009a; Attwood et al., 2016). The intertidal zone consists of rocky and sandy shores as well as deep rockpools, exposed reefs, sand-stone headlands, rounded boulders, and wave-cut limestone platforms (Spencer et al., 2016).

Goukamma's ichthyofaunal community structure has been surveyed using CAS and UVC techniques (Götz, 2005; Pradervand & Hiseman, 2006; Götz et al., 2009b; van Zyl, 2011; Kerwath et al., 2013; Attwood et al., 2016). These studies have identified nine prominent species of fish in the area's inshore and offshore zones: blacktail (*Diplodus capensis*), blue hottentot (*Pachymetopon aeneum*), fransmadam (*Boopsoidea inornata*), galjoen (*Dichistius capensis*), roman (*Chrysoblephus laticeps*), spotted grunter (*Pomadasys commersonnii*), steentjie (*Spondyliosoma emarginatum*), strepie (*Sarpa salpa*), and slender baardman (*Umbrina robinsoni*). *C. laticeps*, *Dichistius capensis*, *P. aeneum*, *P. commersonnii*, and *U. robinsoni* are coveted by recreational anglers for sport and eating. *C. laticeps* and *P. aeneum* are also of value to commercial fisheries (Lamberth & Joubert, 2014). All nine of these species are edible and of worth to subsistence fishermen.

C. laticeps is listed as near threatened on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species and was severely depleted throughout its distribution as a result of overfishing (Mann et al., 2014a). Ten years after the GMPA's establishment the CPUE of *C. laticeps* in the surrounding exploitable waters was found to be double that of pre-MPA rates (Kerwath et al., 2013). It was also determined that the establishment of the GMPA did not negatively affect the catch rates or travel distances of local fishermen. The GMPA already stands as an example of how MPAs can be used to rejuvenate overexploited populations whilst simultaneously benefitting fishermen through the spillover effect (Götz, 2005), and is an ideal candidate to showcase BRUV as a suitable addition to CAS and UVC in MPA monitoring.

1.7 Aims of this study

The GMPA and surrounding area were resurveyed using BRUV in an effort to:

1. Update the pre-existing survey data, to compare BRUV, CAS, and UVC.
2. Lay a foundation for future BRUV monitoring.
3. Evaluate the proposed changes to the GMPA's boundaries.
4. Compare the findings with other MPAs along the south coast.

In Chapter 2 patterns in Goukamma's ichthyofaunal community were described by interpreting a five-year BRUV data set from the MPA and surrounding area. The following questions were answered:

1. Are there differences in species composition among the proposed and pre-existing zones?
2. Does the GMPA's proposed new no-take zone (NNTZ) include more reef fish than the proposed new exploited zone (NEZ)?
3. Is species composition and relative abundance affected by the zones' physical and environmental variables?
4. Are there distinct fish community types within the GMPA and surrounding waters? Do BRUVs record a different species composition to CAS and UVC?

In Chapter 3 the GMPA data were compared to BRUV data from three other south coast MPAs: Betty's Bay, Stilbaai, and Tsitsikamma. The following questions were answered:

1. Do fish abundances differ among the study areas? Do fish community structures differ among them?
2. What is the most significant determinant of community structure among them?
3. Does species richness and abundance decrease from east to west along the south coast according to subtropical subtraction?
4. Are these MPAs complementary or do they offer redundancy in protection?

CHAPTER 2: A BRUV survey of Goukamma's ichthyofaunal communities

2.1 Abstract

An extension of the Goukamma Marine Protected Area's (GMPA) seaward boundary and a restructure of its eastern boundary has been suggested to balance the MPA's protected habitat type ratio by increasing the amount of reef protected by the MPA. Five years of baited remote underwater video system data collected in Goukamma between 2013 and 2017 produced 328 successful deployment records. The data were tested to determine whether the suggested restructure of Goukamma's protection zones will increase species richness and abundance in the MPA. Seventy-four fish species from 33 families were recorded throughout the survey. Previous studies indicate that two thirds of Goukamma's nine most prominent shallow subtidal species do not associate with sandy substrata, which is currently the GMPA's most predominant protected habitat type. The records were analysed using multi-factor analysis of variance, Kruskal-Wallis, and Wilcoxon signed rank tests to determine whether habitat type, protection status, protection zone, depth zone, and season significantly affected their species richness, relative abundance, and Shannon-Wiener and Simpson's similarity index scores. Multivariate gradient analysis and hierarchical clustering were used to identify distinct community structures and interspecific species associations. Species in Goukamma conformed to four distinct community groups. The first group included the majority of the sparids and was associated with reefs in the exploited zone (EZ) and new no-take zone (NNTZ). The remaining three groups were all associated with protected zones. The species richness and relative abundance of these groups were most significantly determined by habitat type (ANOVA: $F = 191.155$, $P < 0.001$ and $F = 96.111$, $P < 0.001$, respectively; Tukey: $q = -4.41$, $P < 0.001$ and $q = -2.12$, $P < 0.001$, respectively). The reef habitat type supported the most diverse and abundant community structure, and higher reef inclusivity in the GMPA would likely lead to increased spillover into exploitable areas and higher catch per unit effort for recreational anglers and commercial or subsistence fishers. The rezoning of the new no-take zone and new exploited zone would be the most effective method of achieving higher reef inclusivity with the lowest risk of impacting local stakeholders exploiting Goukamma's western reefs and oyster beds.

2.2 Introduction

The Goukamma Marine Protected Area's (GMPA) boundaries were demarcated to coincide with that of the terrestrial reserve to take advantage of pre-existing management infrastructure due to a lack of spatially referenced subtidal data on the area's marine environment at the time of its implementation. An echo-sounding conducted in 2005 as part of an assessment of the GMPA and its effect on marine community structure and fishery dynamics highlighted an imbalance in the MPA's protected habitat ratio (Figure 3) (Götz, 2005). Approximately 10.4 km^2 (26%) of the GMPA is made up of rocky reef of aeolianite sandstone origin (Tinley, 1985; Götz et al., 2009a), the majority of which is located on the eastern side of the MPA surrounding Walker's Point. The remainder of the protected benthos is predominantly a sandy sediment substrate (Götz, 2005). Despite the fact that sandy sediments are capable of having extremely high species diversities in the presence of ecosystem engineers (Coolen et al., 2015), they harbour less fish diversity and abundance than rocky reefs or seagrass beds (Jenkins & Wheatley, 1998; Guidetti, 2000). The majority of the area's sandy substrata are unvegetated and barren and thus potentially sub-optimal as nursery grounds for reef-associated species.

The bathymetric map produced by the 2005 echo-sounding highlighted large sections of rocky, reef-suited substrata along the seaward and western boundaries, which prompted a suggestion by Götz et al. (2009a) to restructure Goukamma's boundaries to increase the amount of reef protected by the MPA (Figure 4). More than a decade has passed since the proposal, which has yet to be implemented, despite a multitude of studies highlighting the benefits of higher reef inclusivity in MPAs and the subsequent positive spillover of exploitable resources for recreational anglers and commercial fishermen alike (Götz, 2005; Pradervand & Hiseman, 2006; Kerwath et al., 2007a, 2008; Tunley, 2009; van Zyl, 2011; Grüss et al., 2011; Driver et al., 2012; Sink et al., 2012; Chadwick et al., 2014; Spencer et al., 2016).

The proposed expansion of the seaward boundary, referred to as the NNTZ, would more than double the amount of reef under the GMPA's protection (Götz et al., 2009a). The trade-off in the eastern boundary restructuring would result in the currently protected area around Walker's Point, referred to as the NEZ, being re-opened to boat-based angling. Whilst this area does contain an important portion of reef, it equates to less than 30% of what would be gained through the protection of the NNTZ. The NEZ also encompasses the Buffalo Bay slipway, which experiences high levels of boat traffic, whereas the NNTZ would be less affected by everyday anthropogenic activities and pollutants.

The newly proposed boundaries would increase the size of the protected area by 38% (from 40.2 km^2 to 55.5 km^2) and would more than double the amount of protected reef (from 10.4 km^2 to approximately 22.1 km^2) (Figures 4 and 5). The area to the west of the GMPA and NNTZ, referred to as the exploited zone (EZ), also contains a large portion of reef similar to that in the NNTZ, but is a commercially important oyster harvesting zone and would likely further alienate local stakeholders if closed off entirely (Spencer et al., 2016).

BRUV analysis of Goukamma's four protection zones, the EZ, NEZ, NNTZ, and no-take zone (NTZ), will help to determine if Götz et al.'s (2009a) boundary restructure should go ahead as proposed or be amended to better suit the area's ichthyofaunal communities. The increased proportion of reef in the NNTZ suggests that it would harbour more reef fish than the NEZ, and would thus be a suitable trade-off, however, this needs to be confirmed through ichthyofaunal community analysis of both zones.

Of the nine most prominent fish species identified by CAS and UVC surveys conducted in and around the GMPA, six are sparids, a family that favours rocky environments and/or seagrass beds as nursery areas for juvenile recruitment (Harmelin-Vivien et al., 1995). *B. inornata*, *C. laticeps*, *Diplodus capensis*, *P. aeneum*, *S. emarginatum*, and *S. salpa* all associate with rocky reefs and/or seagrass beds (Binohlan & Garilao, 2019; Binohlan & Luna, 2019a; Binohlan & Reyes, 2019a,b,c; Papasissi & Reyes, 2019). The remaining three species, *Dichistius capensis*, *P. commersonnii*, and *U. robinsoni* associate with both substrata (Binohlan & Sampang-Reyes, 2019; Luna & Garilao, 2019; Luna & Sampang-Reyes, 2019). Two thirds of the most prominent species identified by CAS and UVC surveys therefore do not associate with the GMPA's most predominant protected habitat type (i.e. sandy substratum).

Objectives of this chapter include an analysis of the significant determinants of ichthyofaunal community structures in Goukamma, a comparison of these community structures among the proposed and pre-existing protection zones, and a comparison of the BRUV survey to CAS and UVC surveys conducted in Goukamma's surf and shallow subtidal zones.

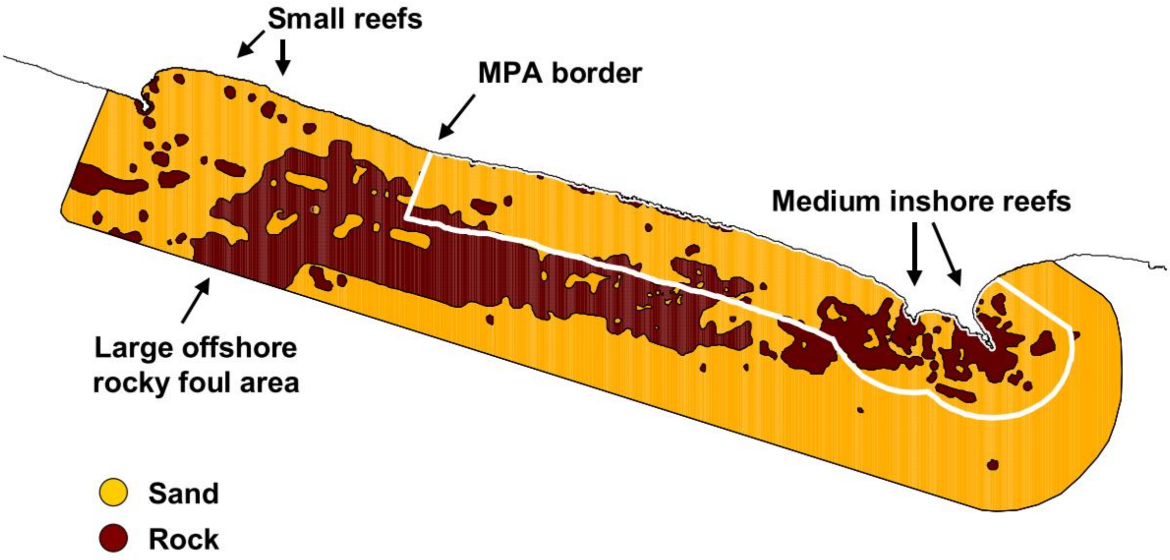

Figure 3: A colour echo-sounding of the Goukamma MPA and surrounding area. Adapted from an *Assessment of the effect of Goukamma Marine Protected Area on community structure and fishery dynamics (Figure 2.5)* (Götz, 2005).

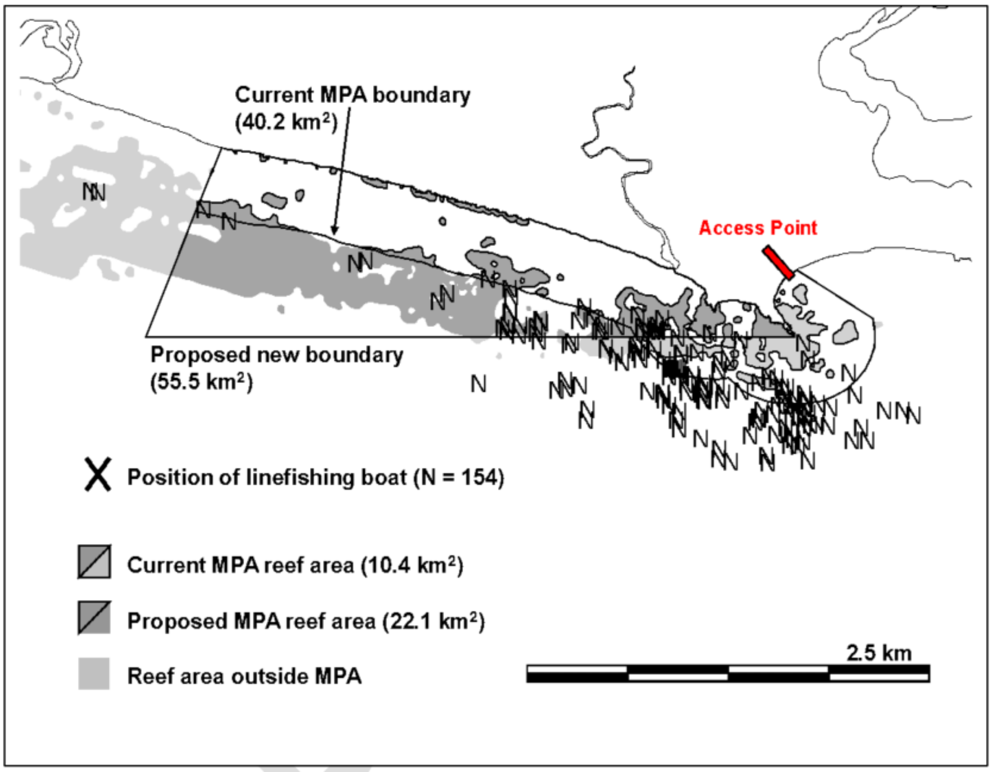

Figure 4: Proposed extension of the Goukamma MPA's seaward boundary (Götz et al., 2009a; Spencer et al., 2016).

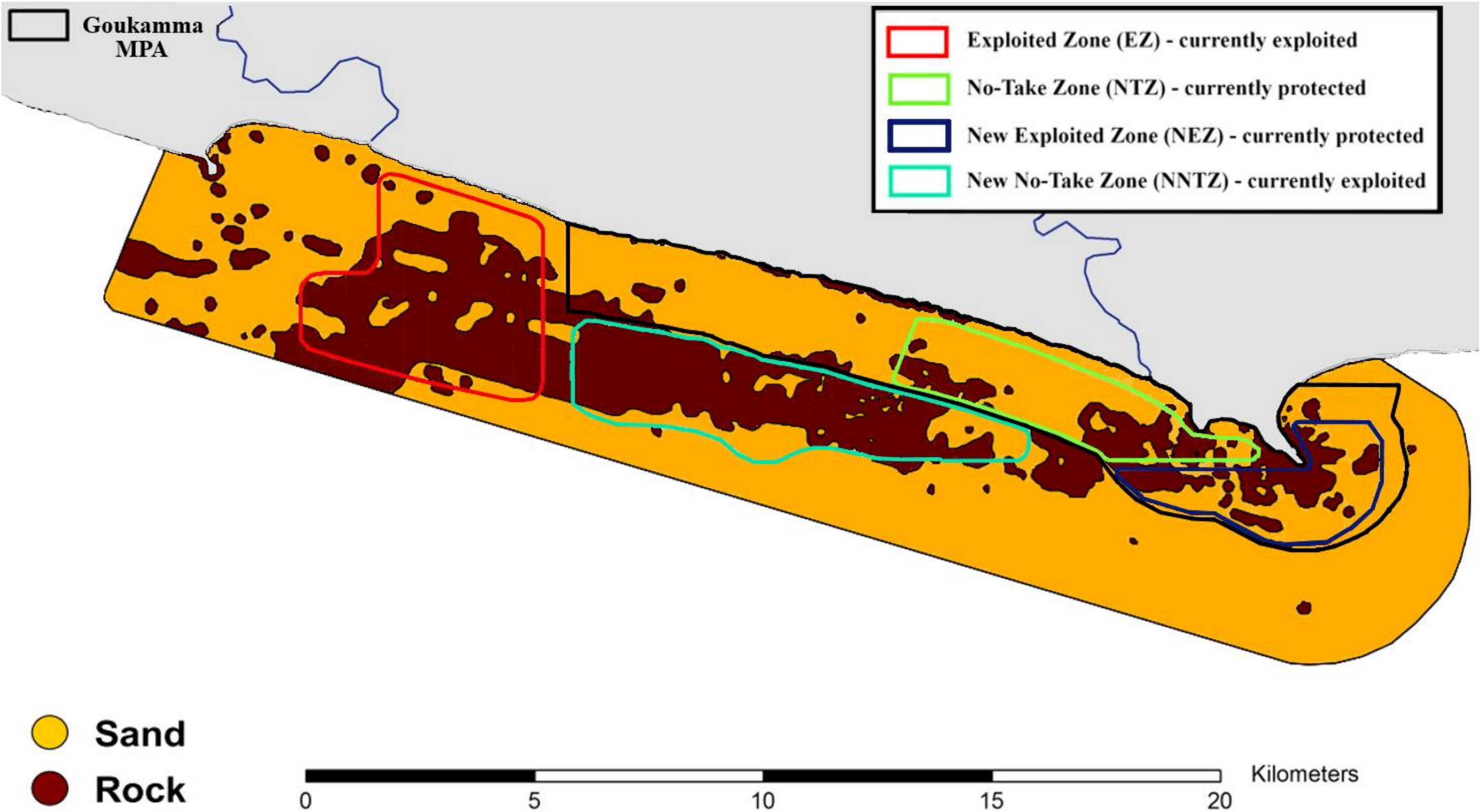

Figure 5: Overlay of echo-sounding data (Figure 3) and the MPA's proposed rezoning (Figure 4) to highlight the proposed shift from predominantly sandy substrata to a higher proportion of reef habitat. The entire MPA prohibits boat-based fishing and is a no-take zone, however, only the eastern half was surveyed during this study, which is specifically referred to as the NTZ. The new exploited and new protected zones (the NEZ and NNTZ respectively) are part of the rezoning proposal and have yet to be implemented (Götz, 2005; Götz et al., 2009a; Spencer et al., 2016).

2.3 Methods

2.3.1 Survey design and BRUV deployments

This survey includes five-years of data collected from 03/07/2013 to 05/05/2017, which amounted to six deployment seasons (Table 3). The sampling target for each season was 64 successful BRUV deployments. Deployments were considered successful when the BRUV rig landed suitably enough for the footage to be analysed (50% or more of the FOV was not obstructed and visibility was 1 m or greater), a minimum of one hour of video footage was recorded, and a minimum of one fish was recorded.

The shallowest depth that BRUVs were deployed to was 5 m and the deepest was 41.5 m. This depth range was considered as Goukamma's shallow subtidal zone. The water column was divided into two separate depth zones: shallow (5-20 m) and deep (20-42 m). Sixteen sites were selected from the EZ, NNTZ, NTZ, and NEZ to achieve the sampling target of 64 successful sites per season. Each protection zone's site selection was designed to be representative of depth zone and habitat type. Two reef sites and two sand sites were randomly selected from the shallow and deep zone of each protection zone, totalling 16 sites per zone. Reef and sand sites were selected based off of Götz's (2005) echo-sounding data (Figure 3).

Deployment seasons were originally intended to be bi-annual (i.e. a summer and a winter season for each year), but staff shortages made this impractical. It was decided from 2014 onwards that data would be collected during summer due to more stable weather conditions. Data collected between 1 June and 30 November were considered as winter samples and data collected between 1 December and 31 May were considered as summer samples.

2.3.2 BRUV design

The BRUV rigs used in Goukamma were constructed according to the guidelines specified in De Vos et al. (2013). The rigs were designed such that the camera is one metre away from the bait cannister and 14 cm above the seafloor (Figure 6). Four BRUVs were used during deployments. The bait used throughout the survey was sardines (*Sardinops sagax*), as is the standard for BRUV surveys in South Africa. Bait cannisters were packed full of chopped *S. sagax* and refilled between successive deployments to maintain consistency of dispersal and olfactory attraction.

Figure 6: The BRUV rig design used in and around the Goukamma MPA.

2.3.3 Data capture

In situ data capture

In situ information included the BRUV rigs' deployment times and the depth and coordinates of each deployment site. Depth was determined using a single beam echosounder. These variables were manually recorded at sea onto field data sheets. Miscellaneous notes on individual deployments were also added to these data sheets where necessary. Field data sheets were digitised in Microsoft® Excel.

Video capture and analysis

Small action GoPro Hero 3 cameras were used in the BRUV rigs due to their relatively low cost, the robustness of their design, and their ability to adjust to highly variable ambient light (Letessier et al., 2015; Bouchet et al., 2018; Langlois et al., 2018). The GoPro's standard video settings were used. Video analysis was conducted on VLC Media Player (*version 2.2.6*

Umbrella). Videos were analysed for a standardised period of one hour following the BRUVs settling on the sea floor.

Determining MaxN and relative abundance

All fish species identified in the videos were recorded and the count at the instance when the highest number of individuals of each species was present in a single frame was recorded as the species' MaxN. This method of determining MaxN mitigates the possibility of recounting the same individuals and inflating species' MaxN counts (Willis et al., 2000). Relative abundance was calculated by summing the MaxN of each species and dividing it by the total number of sites surveyed.

Data-base structure

The deployment details, abiotic variables, and MaxN counts per species were contained in a single record for each BRUV deployment. All records were converted to a comma-separated values (CSV) file format for statistical analysis.

2.3.4 Statistical analysis

All statistical analyses were conducted using R (*version 3.6.1*) in the RStudio integrated design environment. Default parameters were used in all specified functions unless specifically stated. Functions that were used are described in the following format:

The specified analysis and/or figure was produced using the R "function name" function (non-default parameter specification; "*package name*") (package citation).

Distribution maps

Distribution maps were produced using the R ggmap function (*ggmap v3.0.0*) (Kahle & Wickham, 2013) with the geographical coordinates of each deployment site. The ggmap function is used to plot spatial data over static maps from online sources. The cartographic section of the Goukamma MPA and Nature Reserve used in the distribution maps was created using the R get_map function (location = c(22.88, -34.1), zoom = 12; *ggmap v3.0.0*) (Kahle & Wickham, 2013) with the coordinates (22.88; -34.1) and a zoom factor of 12. The get_map function queries online map servers according to specified coordinates.

Explaining variations in diversity and abundance

Habitat type, protection status, protection zone, depth zone, and season were tested to determine whether they affected diversity and abundance in Goukamma. Water temperature and underwater visibility were neither consistently nor reliably measured throughout the five-year data collection period and were therefore excluded from final analyses. Species richness and abundance were selected along with the Shannon-Wiener and Simpson's diversity indices to conduct these analyses. The four dependent variables were species richness, abundance, the Shannon-Wiener index score, and Simpson's index score. The five independent variables were habitat type, protection status, protection zone, depth zone, and season.

Abundance was calculated by summing the MaxN counts for each species. MaxN reduces high volumes of fish to a small number that fits into the FOV. The Shannon-Wiener and Simpson's indices were calculated using the diversity function (index = "Shannon" and index = "Simpson", respectively; *vegan v2.4-2*) (Okansen et al., 2018). Boxplots were used to visually analyse variations in each of the dependent variables as a result of each of the independent variables. The plots were created using the boxplot function (*graphics v3.6.2*). The windows function (*grDevices v3.6.2*) was used to group the dependent variables' boxplots by each of the five independent variables. Each boxplots' coefficient of variation was calculated using the cv function (*goeveg v0.4.2*) (Friedmann & Schellenberg, 2018).

Following visual analysis, each dependent variable's subset of independent variables was tested for homogeneity of variance using Levene's tests. Levene's tests were selected over Bartlett's tests as they allowed for multiple independent variables to be tested simultaneously. The levene_test function (*rstatix v0.3.1*) (Kassambara, 2019) was used to perform these tests.

In cases where all of the variances in a dependent variable's subset of independent variables were homogenous, the independent variables' levels were tested for normality using Shapiro-Wilk tests. The shapiro.test function (*stats v3.6.2*) was used to perform these tests. In cases where the independent variables' levels were normally distributed, multi-factor analysis of variance (ANOVA) tests were used to test the significance of each of the independent variables on the dependent variable. The aov function (*stats v3.6.2*) was used to perform the ANOVA tests. Tukey post hoc tests were used to determine where significant differences existed for independent variables with more than two levels and multi-factor interactions. The TukeyHSD function (*stats v3.6.2*) was used to perform these post hoc tests.

In cases where all of the independent variables' variances were not homogenous or their values were not normally distributed, non-parametric Kruskal-Wallis and Wilcoxon signed-rank tests were used to test the significance of each of the independent variables. Wilcoxon signed-rank tests were used for independent variables with two levels (habitat type, protection status, depth zone, and season) and Kruskal-Wallis tests were used for independent variables with more than two levels (protection zone). The kruskal.test and wilcox.test functions (*stats v3.6.2*) were used to perform these non-parametric tests. Dunn's Multiple Comparison post hoc tests were used to determine where significant differences existed for independent variables with more than two levels. The dunn.test function (*dunn.test v1.3.5*) (Dinno, 2017) was used to perform these post hoc tests.

Determining community structures

The proposed and pre-existing protections zones were tested to determine whether differences existed among their species compositions and whether there were more fish in the NNTZ than in the NEZ.

The method of multivariate gradient analysis (ordination) selected to highlight differences in Goukamma's fish assemblages among sites was canonical analysis of principal coordinates (CAP). CAP was selected over standard redundancy analysis because it allowed for the use of non-Euclidean dissimilarity indices whilst remaining linear and metric (Anderson & Willis, 2003). The dissimilarity index used was the Morisita-Horn index, a modification of Morisita's overlap index, which is a comparative measure of dispersion of individuals in a population that accounts for disproportionate sample size comparisons (Morisita, 1959; Horn, 1966; Chao et al., 2006). When comparing the ordination plots produced by other dissimilarity indices such as the Bray-Curtis and Manhattan indices, the Morisita-Horn index produced the plot with the least cluster overlap and was thus the most interpretable.

The capscale function (distance = "horn", metaMDS = TRUE; *vegan v2.4-2*) (Okansen et al., 2018) was used to create an ordination plot of the observed community structure at each deployment site in relation to every other deployment site, taking into account the effects of depth, habitat type, and protection status. The capscale function performed a distance-based redundancy analysis of the community data and standardised the data using the metaMDS parameter. The form of standardisation used by the metaMDS parameter was Wisconsin double standardisation, which standardises data by dividing each element in a data frame by the maximum value in its column and then further dividing it by the sum of its row (Chizinski, 2016). The ordiselect and ordisurf functions (*vegan v2.4-2*) (Okansen et al., 2018) were used to enhance the interpretability of the ordination plot. The ordiselect function refined the selection of species in the capscale ordination plot based on frequency and relative abundance values. The ordisurf function was used to plot extra graphics, such as depth contours, onto the capscale ordination plot.

Determining interspecific species associations

The species assemblage data at each deployment site were tested to determine whether distinct fish community types existed within Goukamma.

Community types were visually represented using hierarchical clustering to produce a dendrogram. The R hclust function (*stats v3.5.3*) was used to create the dendrogram plot and the cutree function (h = 1.5; *stats v3.5.3*) was used with a cut-off level of 1.5 to group the community clusters. The R vegdist function (method = “horn”; *vegan v2.4-2*) (Okansen et al., 2018) was used to apply the Morisita-Horn index. The R cophenetic function (*stats v3.5.3*) was used to produce a cophenetic correlation coefficient to validate whether the dendrogram was an appropriate summary of the data (Saraçli et al., 2013). The clusters produced were further investigated by comparing published literature on the feeding habits, habitat preferences, and mobility of the species assigned to each grouping.

Comparing species counts and relative abundance data from BRUV, CAS, and UVC surveys conducted Goukamma

The relative abundance means from Götz et al.’s (2009b) CAS and UVC survey of Goukamma’s shallow subtidal zone were compared with BRUV data collected in the same zone. All three data sets were collected over a five-year sampling period. There were too few samples to run analysis of similarities (ANOSIM) or permutational multivariate analysis of variance (PERMANOVA) tests. Each survey methods’ species counts and relative abundance of sparids and chondrichthyans were compared. Overall species counts and relative abundance for each survey method were compared thereafter.

2.4 Results

2.4.1 Ichthyofaunal assessment

Successful BRUV deployments

The goal of 64 successful BRUV deployments was only achieved in the winter of 2014 (Table 3). All other seasons fell short. The lowest was in the summer of 2017. The 2014 data set is more than double the size of the others due to the fact that BRUVs were deployed in summer and winter that year. BRUV deployments were more evenly distributed among depth zones, habitat types, and protection status than seasons and years (Table 4). Over 70% of deployments produced successful data and less than 1% of these successful deployments recorded no fish. Reasons for unsuccessful deployments included inclement weather, reduced visibility as a result of turbidity, and BRUVs getting stuck on the benthos.

Distribution of samples

Figure 7 shows the breakdown between rocky reefs and sandy substrata across the deployment sites. A cluster of reef can be seen in the NEZ around Walker's Point at Buffalo Bay, as shown in Figure 3. The NEZ has a mixed distribution of reef and sandy substrata. The majority of the NTZ sites are sandy substrata, with sections of reef along the NNTZ and NEZ boundaries (south-western and south-eastern boundaries respectively). Over 60% of the surveyed section of the MPA was made up of sandy substrata, and a further 35-40% of the MPA wasn't surveyed, of which the majority is also sand. The majority of the NNTZ and EZ sites are reef.

Figures 8 and 9 show the species richness and abundance ranges across the deployment sites in the form of colour gradient scales. All three figures distinguish between the different protection zones. Higher species richness and abundance appear to correlate with higher prevalence of reef: the lowest averages are seen in the sand dominated NTZ and mixed NEZ.

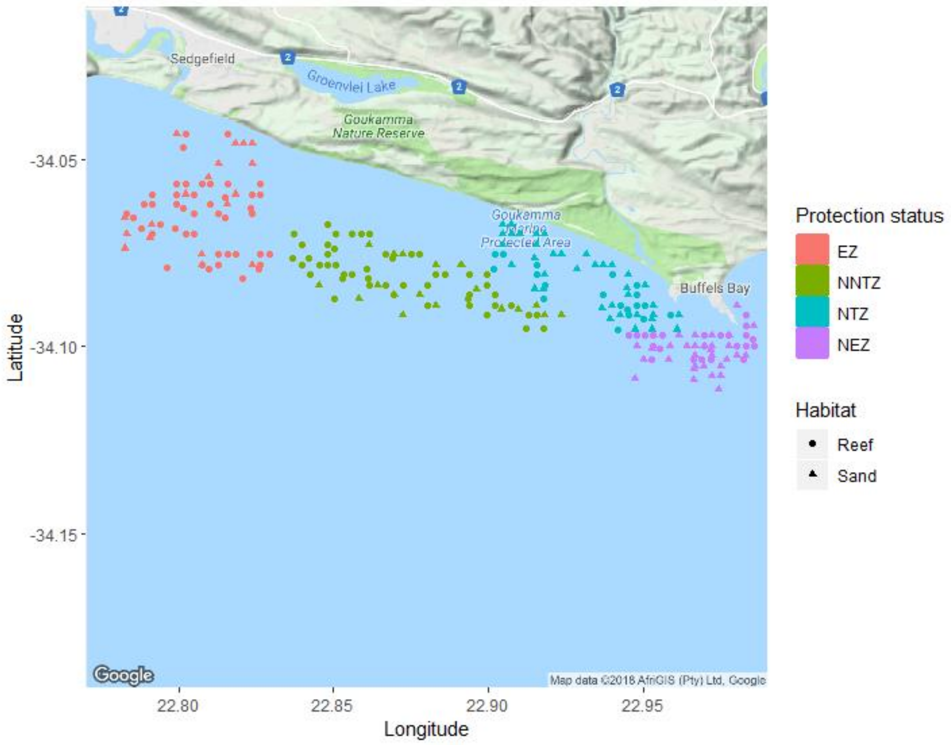

Figure 7: Habitat and protection status of 328 BRUV deployments.

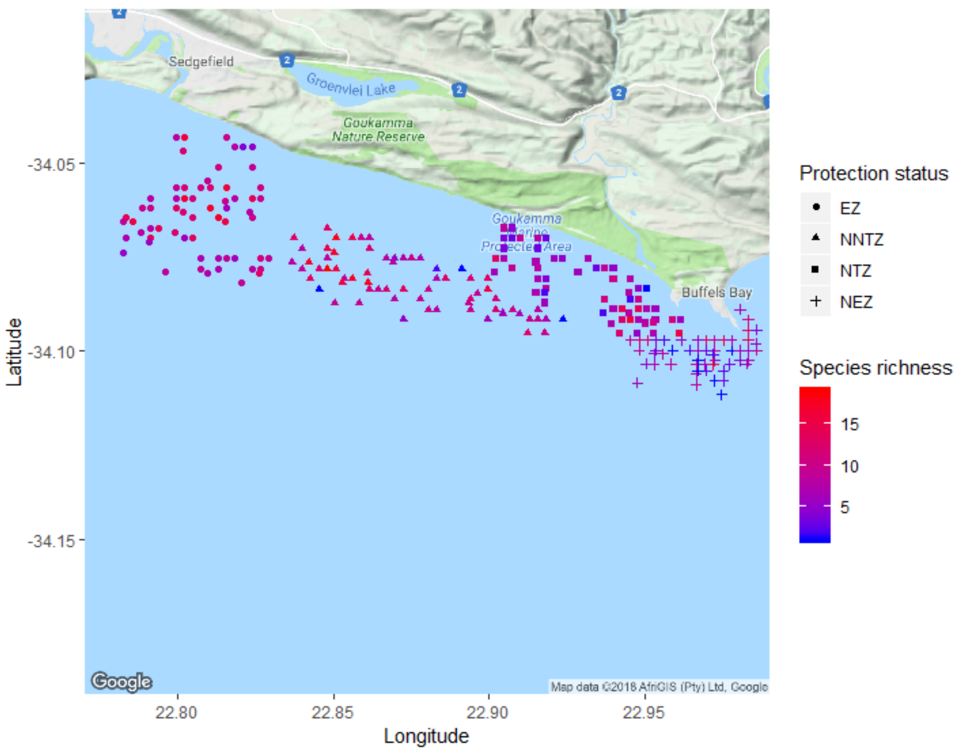

Figure 8: Ichthyofaunal species richness at 328 BRUV deployment sites grouped by protection status.

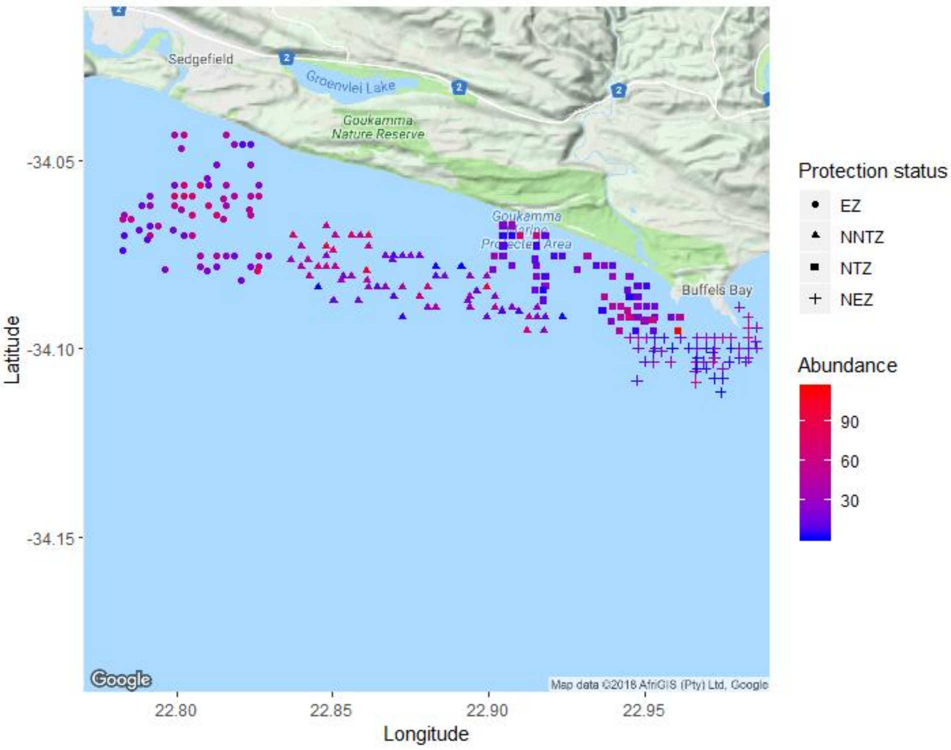

Figure 9: Ichthyofaunal abundance at 328 BRUV deployment sites grouped by protection status.

Table 3: Summary of successful BRUVs in Goukamma from 2013 to 2017.

Variable	No. of successful deployments	% of total
Summer (S)	201	61.3
Winter (W)	127	38.7
2013 (W)	62	18.9
2014 (S)	56	17.1
2014 (W)	65	19.8
2015 (S)	49	14.9
2016 (S)	63	19.2
2017 (S)	33	10.1
Exploited	153	46.6
Protected	175	54.4
EZ	75	22.9
NNTZ	78	23.8
NTZ	91	27.7
NEZ	84	25.6
Reef	184	56.1
Sand	144	43.9
Shallow	140	42.7
Deep	188	57.3

The two highest average abundances of fish per BRUV deployment were observed in the 2013 and 2014 winter surveys (Table 4). The 2016 summer survey showed a higher average number of fish per deployment than the 2014, 2015, and 2017 summer surveys. At least 67% of the total recorded species richness was observed each season (51-58 species per season), except for the summer of 2017. A 21.4% increase in the mean number of fish per site was observed between the 2014-2016 summer seasons, increasing from 28 to 34 over the course of the three years.

Table 4: Variations in BRUV deployments in Goukamma from 2013 to 2017.

Year	Species	Summed abundance	Mean			
			No. of species per site	No. of fish per site	Shannon-Wiener index	Simpson's index
2013 (W)	54	2 278	9	37	1.66	0.72
2014 (S)	49	1 586	9	28	1.63	0.70
2014 (W)	53	2 321	9	36	1.51	0.65
2015 (S)	53	1 496	10	25	1.77	0.74
2016 (S)	57	2 130	9	34	1.67	0.73
2017 (S)	42	754	7	22	1.45	0.67

Summary of the observed ichthyofauna

Thirty-three ichthyofaunal families were recorded over the five-year study period (Table 5). The average number of species identified per family was two, however, this is likely influenced by the Sparidae, which had more than double the number of observed species than the next largest family. Over 60% of the families only had a single species representative.

Sparids accounted for over 25% of species richness and 70% of the total abundance and scyliorhinids accounted for over 8% of species richness and 9% the of total abundance. Cheilodactylids and triakids were the next two most frequently recorded families. The ariids had a comparatively low species count but a comparatively higher relative abundance than other families of similar species counts. Clinids and dichistiids were the only two families where only a single organism was recorded. Highly mobile and migratory chondrichthyan species collectively accounted for over 17% of species richness but made up less than 5% of the total abundance. This included the carcharhinids, dasyatids, hexanchids, lamnids, myliobatids, odontaspidids, sphyrnids, and triakids (Compagno et al., 1991; Duffy & Gordon, 2003; Smale, 2006, 2009; Walker et al., 2006; Casper et al., 2009; Compagno, 2009a,b; Serena et al., 2009; Fergusson et al., 2009; Holtzhausen et al., 2009; Musick et al., 2009; Pollard & Smith, 2009; Duffy et al., 2016).

Table 5: Summary of the ichthyofaunal families observed in and around the Goukamma MPA from 2013 to 2017.

Family	Common name	Species	% of total species richness	Relative abundance	% of total summed abundance
Ariidae	Ariid catfishes	2	2.703	0.955	2.997
Callorhinchidae	Plough-nose chimaeras	1	1.351	0.012	0.038
Carangidae	Jacks, pompanos, and scads	3	4.054	0.52	1.631
Carcharhinidae	Requiem sharks	2	2.703	0.094	0.294
Chaetodontidae	Butterflyfishes	1	1.351	0.054	0.171
Cheilodactylidae	Fingerfins	4	5.405	0.625	1.963
Clinidae	Temperate blennies	1	1.351	0.003	0.009
Dasyatidae	Whiptail stingrays	2	2.703	0.163	0.512
Dichistiidae	Galjoen fishes	1	1.351	0.003	0.009
Gymnuridae	Butterfly rays	1	1.351	0.006	0.019
Haemulidae	Grunts	2	2.703	0.411	1.289
Hexanchidae	Cow sharks	1	1.351	0.030	0.095
Lamnidae	Mackerel sharks	1	1.351	0.015	0.047
Myliobatidae	Eagle rays	1	1.351	0.178	0.56
Myxinidae	Hagfishes	1	1.351	0.012	0.038
Narkidae	Sleeper rays	1	1.351	0.009	0.028
Odontaspididae	Ragged-tooth sharks	1	1.351	0.036	0.114
Oplegnathidae	Knifejaws	1	1.351	0.242	0.759
Parascorpididae	Jutjaws	1	1.351	0.006	0.019
Pomatomidae	Bluefishes	1	1.351	1.25	3.936
Rajidae	Skates	2	2.703	0.066	0.209
Rhinobatidae	Guitarfishes	1	1.351	0.048	0.152
Sciaenidae	Drums/croakers	3	4.054	0.033	0.104
Scyliorhinidae	Catsharks	6	8.108	2.9	9.106
Serranidae	Groupers and seabass	3	4.054	0.314	0.986
Sparidae	Porgies/seabream	19	25.676	22.402	70.331
Sphyrnidae	Hammerhead sharks	1	1.351	0.045	0.142
Squalidae	Dogfishes	1	1.351	0.181	0.569
Tetraodontidae	Pufferfishes	2	2.703	0.535	1.679
Torpedinidae	Electric rays	1	1.351	0.006	0.019
Triakidae	Houndsharks	4	5.405	0.737	2.314

Table 5 (continued): Summary of the ichthyofaunal families observed in and around the Goukamma MPA from 2013 to 2017.

Family	Common name	Species	% of total species richness	Relative abundance	% of total summed abundance
Triglidae	Gurnards	1	1.351	0.012	0.038
Tripterygiidae	Triplefin blennies	1	1.351	0.009	0.028

Seventy-four species and 10 543 fish were recorded over the five-year study period (Table 6). Sixteen of these species are listed as threatened on the IUCN Red List of Threatened Species. The two most frequently recorded species were *Chrysoblephus laticeps* and *Poroderma africanum*. The two species with the highest relative abundances were *Boopsoidea inornata* and *Spondyliosoma emarginatum*. These four species were the only species recorded in over 50% of BRUV deployments. Over 37% of the species identified throughout the survey were chondrichthyans.

Table 6: Summary of the species recorded on BRUVs in and around the Goukamma MPA from 2013 to 2017.

Species	Common name	Family	Original description	Frequency of observation	Relative abundance
Galeichthys ater	Black seacatfish	Ariidae	Castelnau, 1861	67	0.375
Galeichthys feliceps	White seacatfish	Ariidae	Valenciennes, 1840	104	0.58
Callorhinchus capensis	Cape elephantfish	Callorhinchidae	Duméril, 1865	4	0.012
Lichia amia	Garrick	Carangidae	(Linnaeus, 1758)	1	0.003
Seriola lalandi	Giant yellowtail	Carangidae	Valenciennes, 1833	3	0.121
Trachurus trachurus	Atlantic horse mackerel	Carangidae	Castelnau, 1861	7	0.396
Carcharhinus brachyurus	Bronze whaler	Carcharhinidae	(Günther, 1870)	9	0.042
Carcharhinus obscurus	Dusky shark	Carcharhinidae	(Lesueur, 1818)	11	0.051
Chaetodon marleyi	Doublesash Butterflyfish	Chaetodontidae	Regan, 1921	14	0.054
Cheilodactylus fasciatus	Redfingers	Cheilodactylidae	Lacepède, 1803	21	0.082
Cheilodactylus pixi	Barred fingerfin	Cheilodactylidae	Smith, 1980	40	0.154
Chirodactylus brachydactylus	Two-tone fingerfin	Cheilodactylidae	(Cuvier, 1830)	83	0.378
Chirodactylus grandis	Bank steenbras	Cheilodactylidae	(Günther, 1860)	4	0.012
Clinus superciliosus	Highfin clinid	Clinidae	(Linnaeus, 1758)	1	0.003

Table 6 (continued): Summary of the species recorded on BRUVs in and around the Goukamma MPA from 2013 to 2017.

Species	Common name	Family	Original description	Frequency of observation	Relative abundance
Bathytoshia brevicaudata	Short-tail stingray	Dasyatidae	(Hutton, 1875)	39	0.145
Dasyatis chrysonota	Blue stingray	Dasyatidae	(Smith, 1828)	6	0.018
Dichistius capensis	Galjoen	Dichistiidae	(Cuvier, 1831)	1	0.003
Gymnura natalensis	Diamond butterfly ray	Gymnuridae	(Gilchrist & Thompson, 1911)	2	0.006
Pomadasys olivaceus	Piggy	Haemulidae	(Day, 1875)	23	0.408
Pomadasys striatus	Striped grunter	Haemulidae	(Gilchrist & Thompson, 1908)	1	0.003
Notorynchus cepedianus	Spotted sevengill shark	Hexanchidae	(Péron, 1807)	10	0.03
Carcharodon carcharias	Great white shark	Lamnidae	(Linnaeus, 1758)	5	0.015
Myliobatis aquila	Common eagle ray	Myliobatidae	(Linnaeus, 1758)	51	0.178
Eptatretus hexatrema	Sixgill hagfish	Myxinidae	(Müller, 1836)	4	0.012
Narke capensis	Onefin electric ray	Narkidae	(Gmelin, 1789)	2	0.009
Carcharias taurus	Ragged-tooth shark	Odontaspididae	Rafinesque, 1810	12	0.036
Oplegnathus conwayi	Cape knifejaw	Oplegnathidae	Richardson, 1840	47	0.242
Parascorpis typus	Jutjaw	Parascorpididae	Bleeker, 1875	1	0.006
Pomatomus saltatrix	Shad	Pomatomidae	(Linnaeus, 1766)	14	1.254
Raja straeleni	Biscuit skate	Rajidae	Poll, 1951	4	0.012
Rostroraja alba	Spearnose skate	Rajidae	(Lacepède, 1803)	17	0.054
Acroteriobatus annulatus	Lesser guitarfish	Rhinobatidae	(Müller & Henle, 1841)	16	0.048
Argyrosomus japonicus	Dusky kob	Sciaenidae	(Temminck & Schlegel, 1843)	2	0.006
Atractoscion aequidens	Geelbek	Sciaenidae	(Cuvier, 1830)	4	0.024
Umbrina robinsoni	Slender baardman	Sciaenidae	Valenciennes, 1843	1	0.003
Halaelurus natalensis	Tiger catshark	Scyliorhinidae	(Regan, 1904)	31	0.1
Haploblepharus edwardsii	Puffadder shyshark	Scyliorhinidae	(Schinz, 1822)	74	0.269
Haploblepharus fuscus	Brown shyshark	Scyliorhinidae	Smith, 1950	31	0.097
Poroderma africanum	Striped catshark	Scyliorhinidae	(Gmelin, 1789)	223	1.961
Poroderma pantherinum	Leopard catshark	Scyliorhinidae	(Müller & Henle, 1838)	113	0.471
Scyliorhinus capensis	Yellowspotted catshark	Scyliorhinidae	(Müller & Henle, 1838)	1	0.003
Acanthistius sebastoides	Koester	Serranidae	(Castelnau, 1861)	54	0.184
Epinephelus marginatus	Yellowbelly rockcod	Serranidae	(Lowe, 1834)	27	0.1
Serranus cabrilla	African seabass	Serranidae	(Linnaeus, 1758)	9	0.030
Boopsoidea inornata	Fransmadam	Sparidae	Castelnau, 1861	172	3.87

Table 6 (continued): Summary of the species recorded on BRUVs in and around the Goukamma MPA from 2013 to 2017.

Species	Common name	Family	Original description	Frequency of observation	Relative abundance
Cheimerius nufar	Santer	Sparidae	(Valenciennes, 1830)	153	1.054
Chrysoblephus cristiceps	Dageraad	Sparidae	(Valenciennes, 1830)	58	0.263
Chrysoblephus gibbiceps	Red stumpnose	Sparidae	(Valenciennes, 1830)	75	0.263
Chrysoblephus laticeps	Roman	Sparidae	(Valenciennes, 1830)	227	3.181
Cymatoceps nasutus	Black musselcracker	Sparidae	(Castelnau, 1861)	1	0.003
Diplodus capensis	Blacktail	Sparidae	(Smith, 1844)	73	0.616
Diplodus hottentotus	Zebra	Sparidae	(Smith, 1844)	81	0.36
Gymnocrotaphus curvidens	Janbruin	Sparidae	Günther, 1859	25	0.082
Lithognathus mormyrus	Sand steenbras	Sparidae	(Linnaeus, 1758)	14	0.115
Pachymetopon aeneum	Blue hottentot	Sparidae	(Gilchrist & Thompson, 1908)	132	1.498
Pachymetopon grande	Bronze seabream	Sparidae	Günther, 1859	5	0.024
Pagellus natalensis	Red tjor-tjor	Sparidae	Steindachner, 1903	60	0.885
Petrus rupestris	Red steenbras	Sparidae	(Valenciennes, 1830)	57	0.181
Polysteganus undulosus	Seventy-four	Sparidae	(Regan, 1908)	5	0.015
Pterogymnus laniarius	Panga	Sparidae	(Valenciennes, 1830)	64	0.468
Rhabdosargus holubi	Cape stumpnose	Sparidae	(Steindachner, 1881)	2	0.009
Sarpa salpa	Strepie	Sparidae	(Linnaeus, 1758)	9	0.384
Spondyliosoma emarginatum	Steentjie	Sparidae	(Valenciennes, 1830)	196	9.13
Sphyrna zygaena	Smooth hammerhead	Sphyrnidae	(Linnaeus, 1758)	14	0.045
Squalus megalops	Shortnose spiny dogfish	Squalidae	(MacLeay, 1881)	27	0.181
Amblyrhynchotes honckenii	Evileye puffer	Tetraodontidae	(Bloch, 1785)	63	0.526
Lagocephalus sceleratus	Silver-cheeked Toadfish	Tetraodontidae	(Gmelin, 1789)	2	0.009
Torpedo fuscomaculata	Blackspotted torpedo	Torpedinidae	Peters, 1855	2	0.006
Galeorhinus galeus	Soupfin shark	Triakidae	(Linnaeus, 1758)	14	0.045
Mustelus mustelus	Common smooth-hound	Triakidae	(Linnaeus, 1758)	141	0.637
Mustelus palumbes	Whitespotted smooth-hound	Triakidae	Smith, 1957	5	0.018
Triakis megalopterus	Spotted gully shark	Triakidae	(Smith, 1839)	8	0.036
Chelidonichthys kumu	Bluefin gurnard	Triglidae	(Cuvier, 1829)	4	0.012
Cremnochorites capensis	Cape triplefin	Tripterygiidae	(Gilchrist & Thompson, 1908)	3	0.009

2.4.2 Variations in diversity and total abundance

2.4.2.1 Visual interpretation of diversity and abundance boxplots

Habitat type

Samples from reef sites had an average of 22% more species and 33% more fish than samples from sand sites (Figure 10). Reef samples were on average 21% more diverse on the Shannon-Wiener index and 12% more diverse on Simpson's index than sand samples. Interquartile ranges were similar for species richness and abundance but were smaller for reef samples on the Shannon-Wiener and Simpson's indices. Sand samples had higher coefficients of variation than reef samples (Table 7).

Protection status

Samples from exploited sites had an average of 22% more species and 24% more fish than samples from protected sites (Figure 11). Exploited samples were on average 12% more diverse on the Shannon-Wiener index and 12% more diverse on Simpson's index than protected samples. Interquartile ranges were similar for species richness and abundance but were smaller for exploited samples on the Shannon-Wiener and Simpson's indices. Protected samples had higher coefficients of variation than exploited samples (Table 7).

Protection zone

Samples from the EZ had an average of 10% more species than samples from the NNTZ and 20% more species than samples from the NTZ and NEZ (Figure 12). EZ samples had an average of 17% more fish than NNTZ samples, 33% more fish than NTZ samples, and 7% more fish than NEZ samples. EZ samples were on average 7% less diverse than NNTZ samples, 6% more diverse than NTZ samples, and 14% more diverse than NEZ samples on the Shannon-Wiener index. EZ samples were on average 4% less diverse NNTZ samples, 1% less diverse than NTZ samples, and 10% more diverse than NEZ samples on Simpson's index.

The interquartile ranges for species richness were similar for samples from the EZ, NNTZ, and NEZ and smaller for samples from the NTZ. The interquartile ranges for abundance were similar for samples from the EZ, NTZ, and NEZ and smaller for samples from the NNTZ. The interquartile ranges for both diversity indices were similar for samples from the EZ, NNTZ, and NTZ and larger for samples from the NEZ. NEZ samples had higher coefficients of variation for species richness and both diversity indices' than samples from the other three zones. NTZ samples had the highest coefficient of variation for abundance (Table 7).

Depth zone

Samples from shallow sites had an average of 11% more species and 30% more fish than deep sites (Figure 13). Shallow and deep samples did not differ in diversity on the Shannon-Wiener and Simpson's indices. Interquartile ranges were similar for species richness, abundance, and both diversity indices. Deep samples had higher coefficients of variation than shallow samples (Table 7).

Season

Samples summer sites had an average of 11% less species and 33% less fish than winter samples (Figure 14). Summer and winter samples did not differ in diversity on the Shannon-Wiener and Simpson's indices. Interquartile ranges were similar for species richness, abundance, and both diversity indices. Summer samples had higher coefficients of variation for species richness and abundance but lower coefficients of variation for both diversity indices' than winter samples (Table 7).

Table 7: Coefficients of variation for the habitat type (Figure 10), protection status (Figure 11), protection zone (Figure 12), depth zone (Figure 13), and season (Figure 14) boxplots.

	Species richness	**Abundance**	**Shannon-Wiener index**	**Simpson's index**
		Habitat type		
Reef	0.31	0.55	0.18	0.14
Sand	0.52	1.04	0.45	0.40
		Protection status		
Exploited	0.36	0.62	0.25	0.21
Protected	0.55	0.89	0.39	0.33
		Protection zone		
EZ	0.32	0.55	0.22	0.18
NNTZ	0.40	0.70	0.29	0.26
NTZ	0.48	0.92	0.30	0.21
NEZ	0.62	0.86	0.49	0.43
		Depth zone		
Shallow	0.45	0.70	0.27	0.19
Deep	0.49	0.78	0.38	0.33
		Season		
Summer	0.49	0.81	0.33	0.27
Winter	0.46	0.70	0.34	0.29

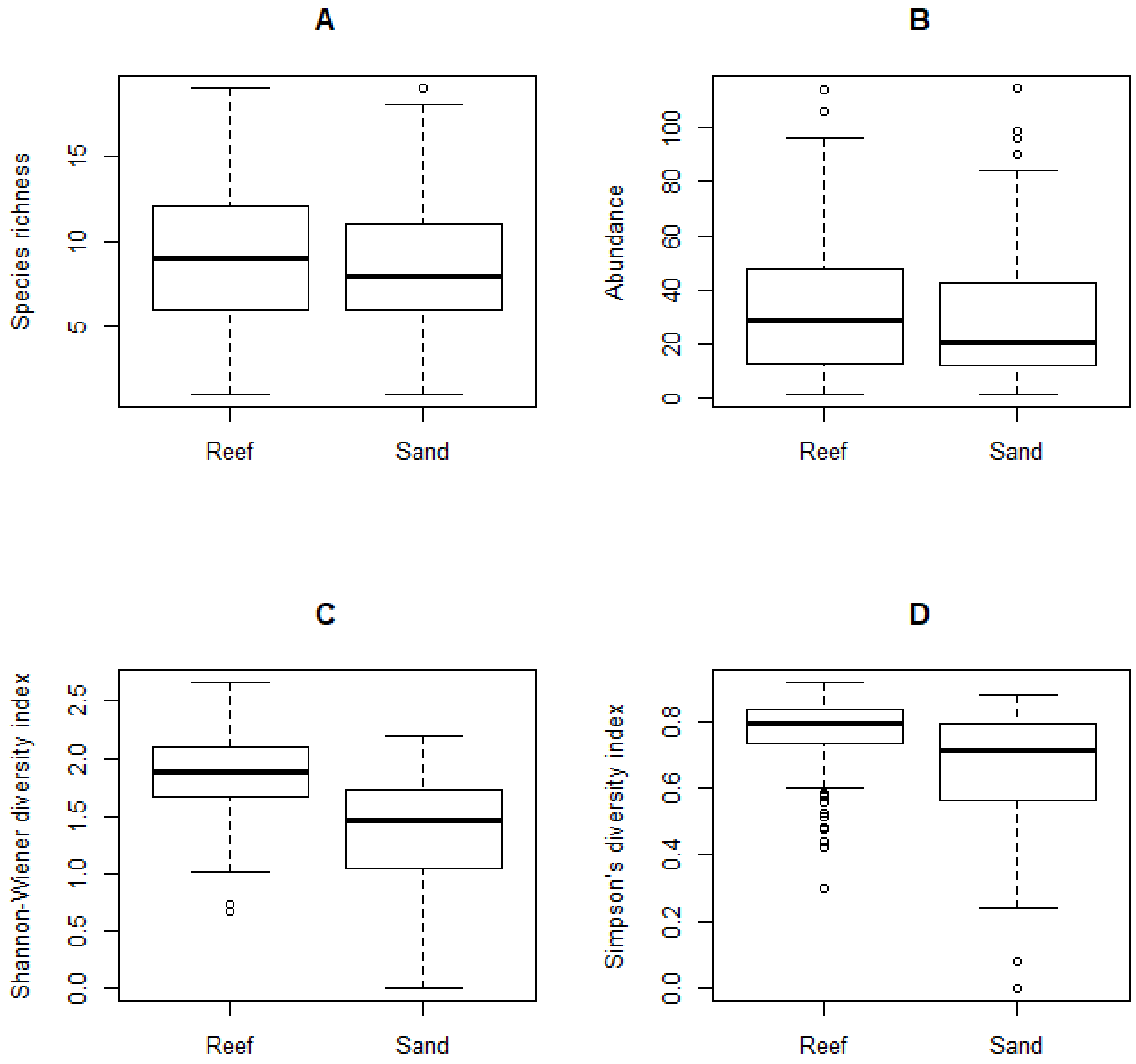

Figure 10: A comparison of species richness (A), abundance (B), the Shannon-Wiener index (C), and Simpson's index (D) between habitat types (184 reef sites and 144 sand sites). Each boxplot shows the median, interquartile range, upper and lower quartile limits, and outliers.

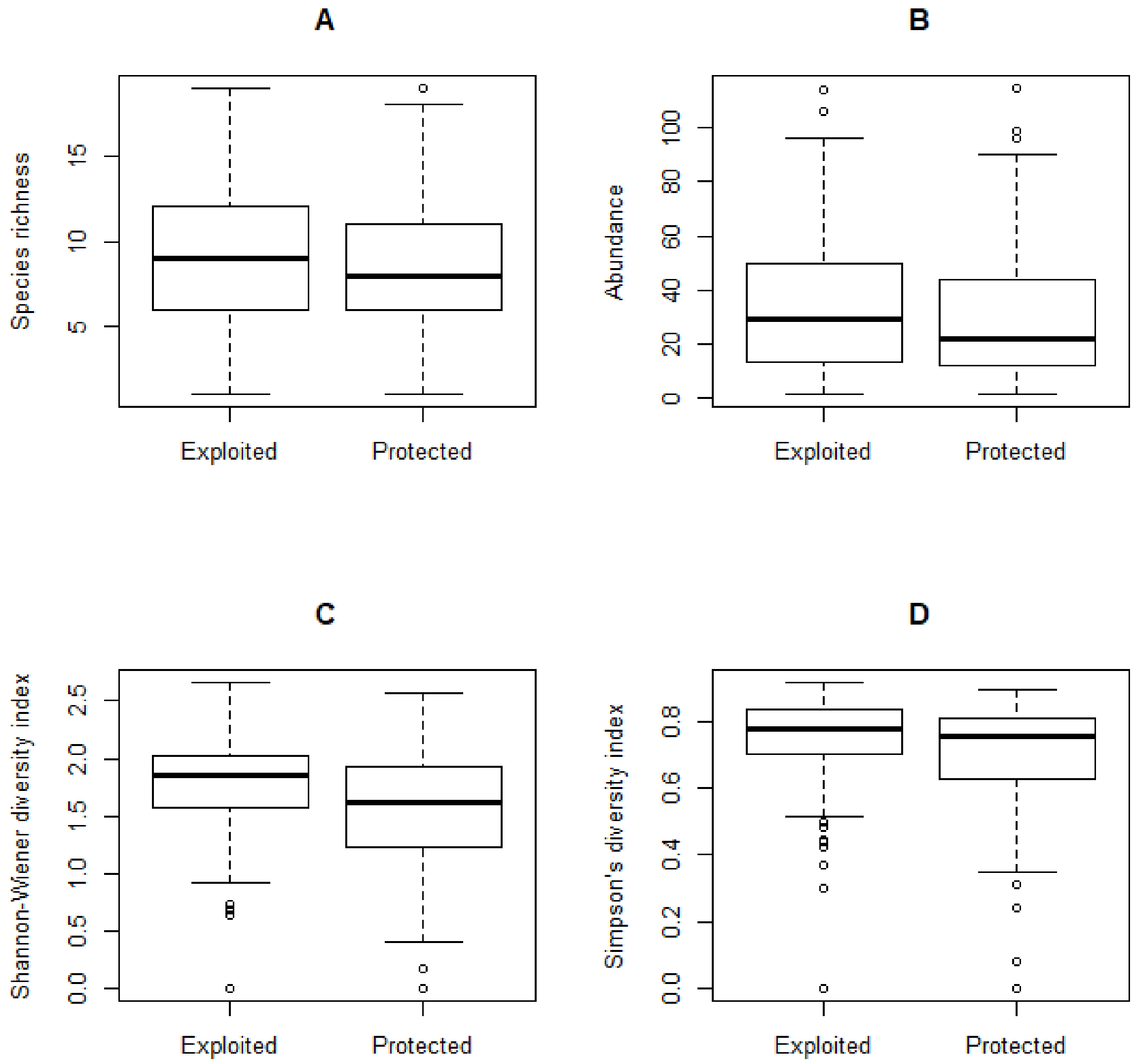

Figure 11: A comparison of species richness (A), abundance (B), the Shannon-Wiener index (C), and Simpson's index (D) between protection status (153 exploited sites and 175 protected sites). Each boxplot shows the median, interquartile range, upper and lower quartile limits, and outliers.

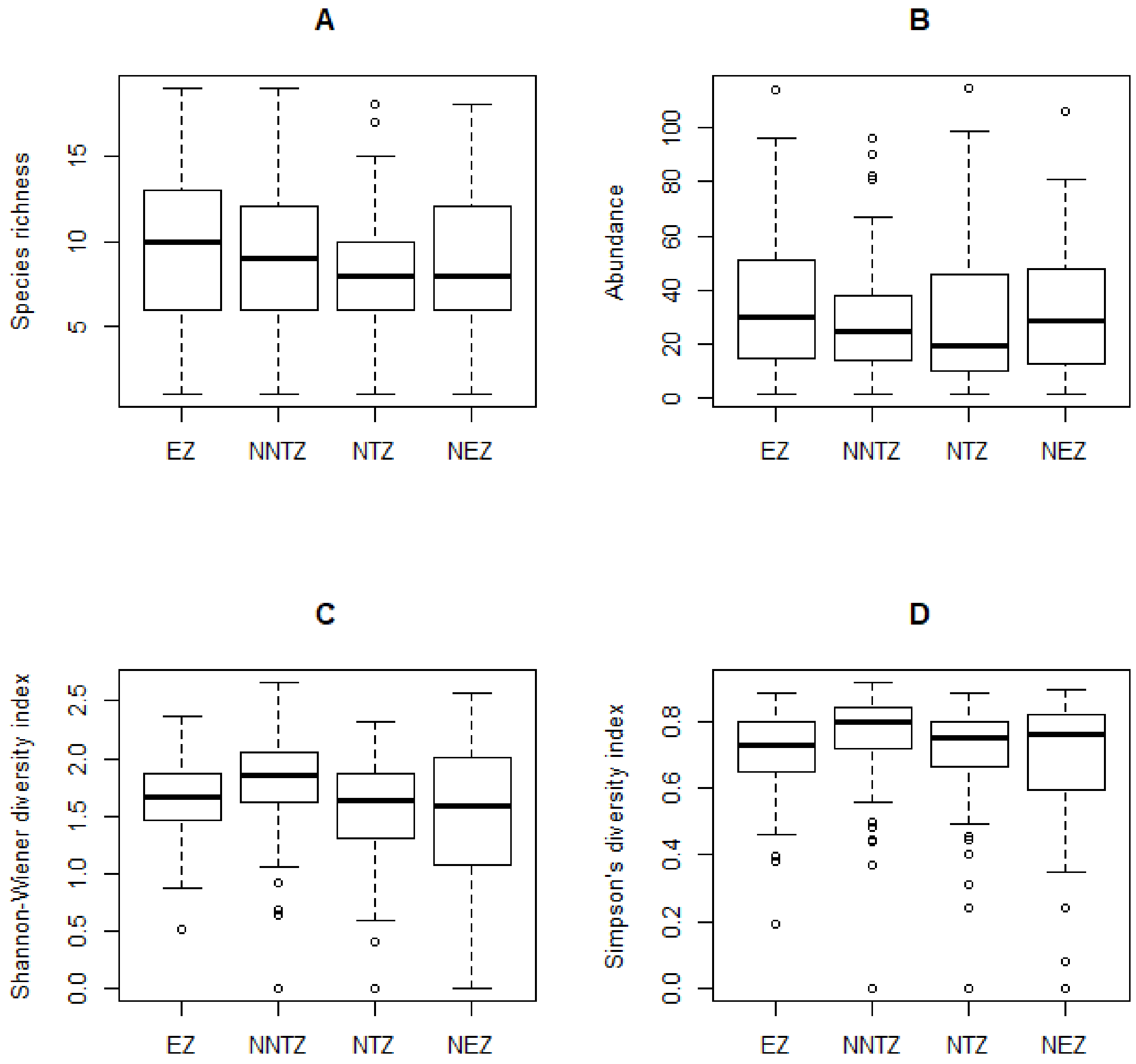

Figure 12: A comparison of species richness (A), abundance (B), the Shannon-Wiener index (C), and Simpson's index (D) among protection zones (75 exploited zone sites, 78 new no-take zone sites, 91 no-take zone sites, and 84 new exploited zone sites). Each boxplot shows the median, interquartile range, upper and lower quartile limits, and outliers.

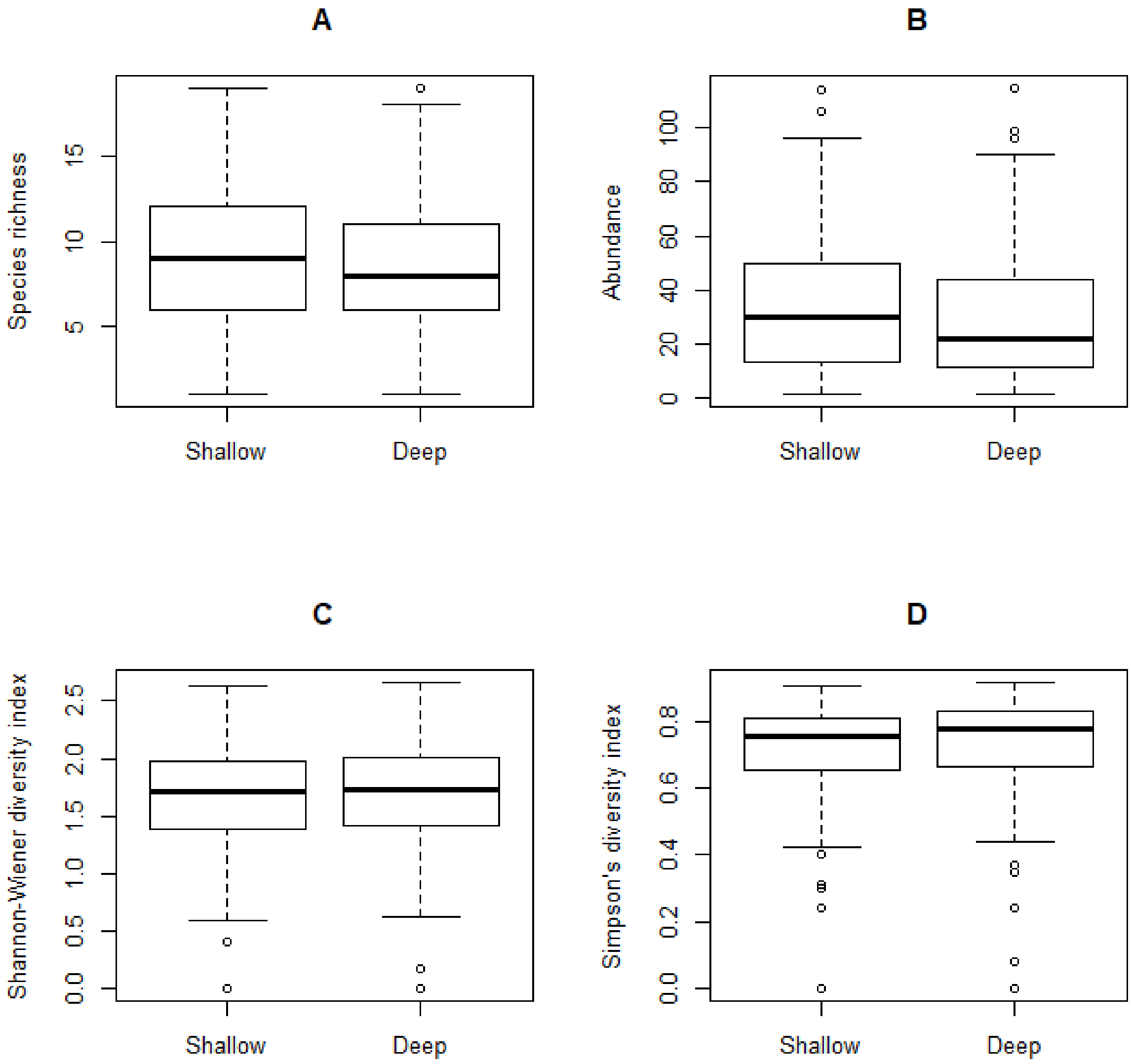

Figure 13: A comparison of species richness (A), abundance (B), the Shannon-Wiener index (C), and Simpson's index (D) between depth zones (140 shallow sites and 188 deep sites). Each boxplot shows the median, interquartile range, upper and lower quartile limits, and outliers.

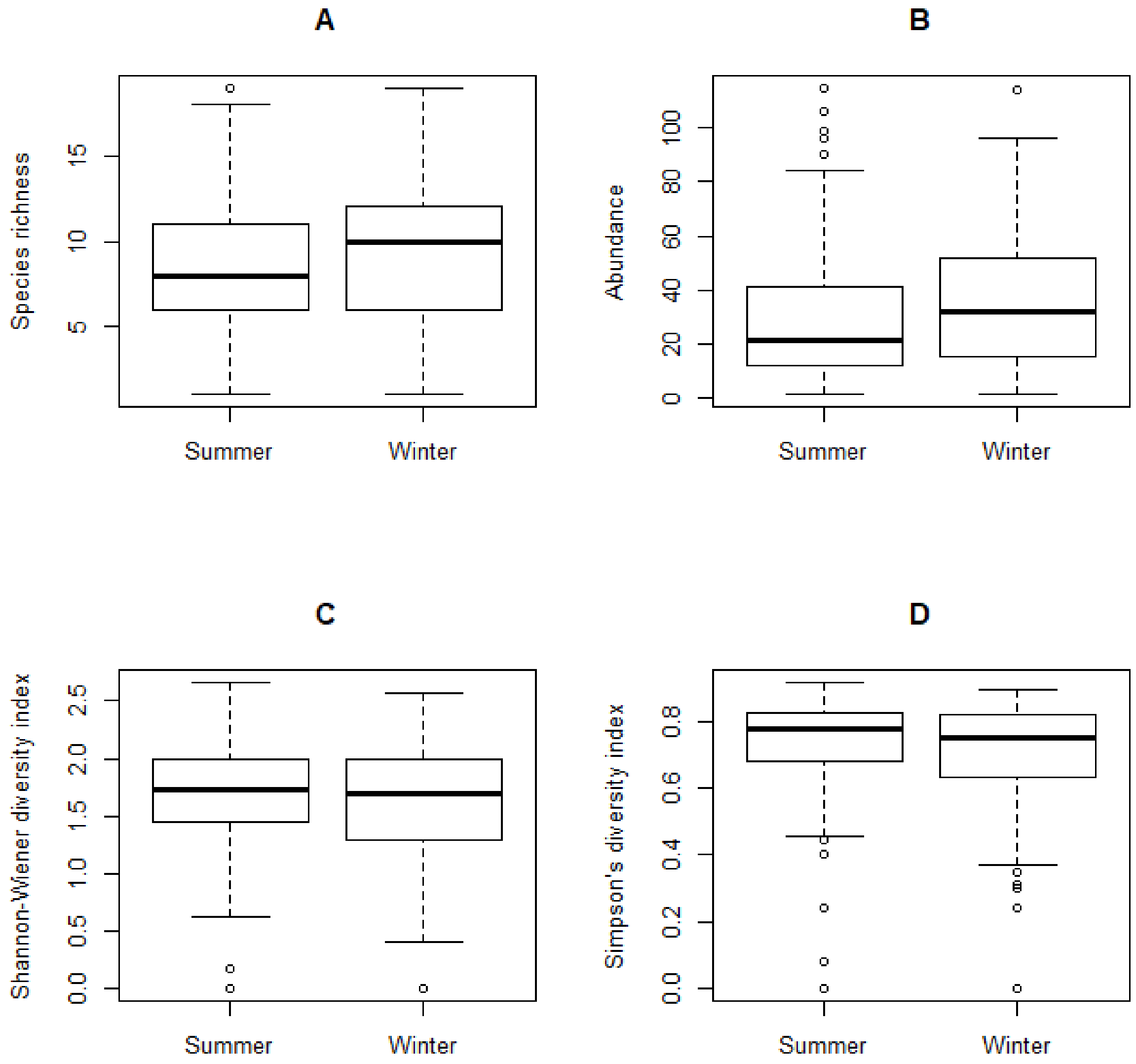

Figure 14: A comparison of species richness (A), abundance (B), the Shannon-Wiener index (C), and Simpson's index (D) among seasons (201 summer sites and 127 winter sites). Each boxplot shows the median, interquartile range, upper and lower quartile limits, and outliers.

2.4.2.2 Assumption tests and significance models

Variances were homogenous among all levels of the four independent variables of species richness and abundance (Levene: $W = 1.40$, $P = 0.865$ and $W = 1.26$, $P = 0.169$, respectively). Four-way ANOVA tests were used to compare each dependent variable across the different levels of independent variables. Protection status is confounded with protection zone, which is why it was omitted from the ANOVAs (Tables 9 and 10).

Variances were not homogenous among all levels of the five independent variables of the Shannon-Wiener and Simpson's indices (Levene: $W = 2.75$, $P = 6.99 \times 10^{-6}$ and $W = 3.30$, $P = 8.4 \times 10^{-8}$, respectively). Non-parametric Kruskal-Wallis and Wilcoxon signed rank tests were used to separately compare the diversity among the various levels of the factors listed above.

Habitat type

Species richness and abundance each significantly differed between reef and sand sites (ANOVA: $F = 191.155$, $P < 2 \times 10^{-16}$ and $F = 96.111$, $P < 2 \times 10^{-16}$, respectively). Reef sites had significantly higher species richness and abundance than sand sites (Tukey: $q = -4.41$, $P < 1.00 \times 10^{-7}$ and $q = -2.12$, $P < 1.00 \times 10^{-7}$, respectively).

Variances of the Shannon-Wiener and Simpson's indices were not homogenous between the two levels of habitat type (Levene: $W = 28.170$, $P = 2.06 \times 10^{-8}$ and $W = 35.000$, $P = 8.33 \times 10^{-9}$, respectively). Reef sites were significantly more diverse than sand sites on both indices (Wilcox: $W = 21\,102$, $P < 2.2 \times 10^{-16}$ and $W = 18\,553$, $P = 4.85 \times 10^{-10}$, respectively).

Protection status

Species richness and abundance each significantly differed between exploited and protected sites (ANOVA: $F = 27.740$, $P = 7.65 \times 10^{-16}$ and $F = 10.438$, $P = 1.51 \times 10^{-6}$, respectively). Variances of the Shannon-Wiener and Simpson's indices were not homogenous between the two levels of protection status (Levene: $W = 9.62$, $P = 2.10 \times 10^{-3}$ and $W = 4.8$, $P = 0.0292$, respectively). Exploited sites were significantly more diverse than protected sites on both indices (Wilcox: $W = 17\,314$, $P = 4.58 \times 10^{-6}$ and $W = 15\,896$, $P = 3.42 \times 10^{-3}$, respectively).

Protection zone

Species richness and abundance each significantly differed among the EZ, NNTZ, NTZ, and NEZ (ANOVA: $F = 27.740$, $P = 7.65 \times 10^{-16}$ and $F = 10.438$, $P = 1.51 \times 10^{-6}$, respectively). The EZ had significantly more species and fish than the NEZ (Tukey: $q = -3.23$, $P < 1.00 \times 10^{-7}$ and $q = -1.16$, $P = 2.58 \times 10^{-3}$, respectively) and NTZ (Tukey: $q = -3.07$, $P < 1.00 \times 10^{-7}$ and $q = -1.04$, $P = 7.84 \times 10^{-3}$, respectively). The NNTZ similarly had significantly more species and fish than the NEZ (Tukey: $q = 3.07$, $P < 1.00 \times 10^{-7}$ and Tukey: $q = 1.48$, $P < 1.00 \times 10^{-7}$ 0, respectively) and NTZ (Tukey: $q = -2.91$, $P < 1.00 \times 10^{-7}$ 0 and $q = -1.35$, $P = 1.74 \times 10^{-4}$, respectively).

Variances of the Shannon-Wiener and Simpson's indices were not homogenous among the four levels of protection zone (Levene: $W = 8.01$, $P = 3.63 \times 10^{-5}$ and $W = 5.43$, $P = 1.18 \times 10^{-3}$, respectively). Significant differences existed among the diversities of the protection zones on both indices (Kruskal-Wallis: $\chi^2 = 21.5$, df = 3, $P = 8.27 \times 10^{-5}$ and $\chi^2 = 10.31$, df = 3, $P = 0.0160$, respectively). The EZ had a significantly higher diversity than the NEZ and NTZ (Dunn: $Z = 2.90$, $P = 1.84 \times 10^{-3}$ and $Z = 2.82$, $P = 2.41 \times 10^{-3}$, respectively) on the Shannon-Wiener index, as did the NNTZ (Dunn: $Z = -3.65$, $P = 1.32 \times 10^{-4}$ and $Z = 3.58$, $P = 1.74 \times 10^{-4}$, respectively). The NNTZ had a significantly higher diversity than the NEZ and NTZ on Simpson's index (Dunn: $Z = -2.87$, $P = 2.06 \times 10^{-3}$ and $Z = 2.60$, $P = 4.60 \times 10^{-3}$, respectively)

Depth zone

Species richness significantly differed between exploited and protected sites (ANOVA: $F = 8.656$, $P = 3.52 \times 10^{-3}$). Abundance did not (ANOVA: $F = 0.650$, $P = 0.421$). Shallow sites had significantly higher species richness than deep sites (Tukey: $q = 0.913$, $P = 7.57 \times 10^{-3}$). There was no significant difference in abundance between shallow and deep sites (Tukey: $q = -0.170$, $P = 0.462$).

Variances of the Shannon-Wiener and Simpson's indices were homogenous between the two levels of depth zone (Levene: $W = 9.62$, $P = 2.10 \times 10^{-3}$ and $W = 4.63$, $P = 0.0321$, respectively). However, neither the shallow nor the deep sites' diversities were normally distributed on the Shannon-Wiener index (Shapiro-Wilk: $W = 0.972$, $P = 6.04 \times 10^{-3}$ and $W = 0.868$, $P = 9.99 \times 10^{-12}$, respectively) or Simpson's index (Shapiro-Wilk: $W = 0.848$, $P = 1.02 \times 10^{-10}$ and $W = 0.697$, $P = 3.43 \times 10^{-18}$, respectively). There were no significant differences between the diversities of shallow and deep sites on either index (Wilcox: W = 13 282, $P = 0.885$ and W = 14 472, $P = 0.123$, respectively).

Season

Neither species richness nor abundance differed significantly between summer and winter (ANOVA: F = 1.300, P = 0.255 and F = 1.500, P = 0.214, respectively). However, species richness was significantly higher in the shallow zone during summer (Tukey: q = 1.65, P = 9.51×10^{-4}).

Variances of the Shannon-Wiener and Simpson's indices were homogenous between the two levels of season (Levene: W = 0.35, P = 0.0556 and W = 0.68, P = 0.409, respectively). However, neither the summer nor the winter sites' diversities were normally distributed on the Shannon-Wiener index (Shapiro-Wilk: W = 0.888, P = 4.32×10^{-11} and W = 0.922, P = 1.67×10^{-6}, respectively) or Simpson's index (Shapiro-Wilk: W = 0.688, P = 4.47×10^{-19} and W = 0.786, P = 2.47×10^{-12}, respectively). There was no significant difference between the diversity of summer and winter sites on either index (Wilcox: W = 13 282, P = 0.885 and W = 14 489, P = 0.391, respectively).

2.4.2.3 Multi-factor ANOVA tables

Table 8: Four-way ANOVA test of species richness.

	Degrees of freedom	Sum of squares	Mean of squares	F value	Probability (> F)	Significance level
Protection zone (PZ)	3	769.8	256.6	27.740	7.65×10^{-16}	***
Habitat type (HT)	1	1 768.2	1 768.2	191.155	$< 2 \times 10^{-16}$	***
Depth zone (DZ)	1	80.1	80.1	8.656	3.52×10^{-3}	**
Season (S)	1	12	12	1.300	0.255	
Two-way comparisons						
PZ:HT	3	48.3	16.1	1.742	0.158	
PZ:DZ	3	17.4	5.8	0.628	0.597	
HT:DZ	1	17.3	17.3	1.873	0.172	
PZ:S	3	122.6	40.9	4.417	4.67×10^{-3}	**
HT:S	1	27.7	27.7	2.993	0.0847	.
DZ:S	1	85.3	85.3	9.22	2.61×10^{-3}	**
Three-way comparisons						
PZ:HT:DZ	3	55.6	18.5	2.005	0.113	
PZ:HT:S	3	27.8	9.3	1.001	0.393	
PZ:DZ:S	3	10.6	3.5	0.382	0.766	
HT:DZ:S	1	0.2	0.2	0.018	0.894	
Four-way comparison						
PZ:HT:DZ:S	2	2	1	0.106	0.899	
Residuals	297	2 747.3	9.3			
Significance key:	"***" = 0.001	"**" = 0.01	"*" = 0.05		"." = 0.1	" " = 1

Table 9: Four-way ANOVA test of abundance.

	Degrees of freedom	Sum of squares	Mean of squares	F value	Probability (> F)	Significance level
Protection zone (PZ)	3	133.7	44.6	10.438	1.51×10^{-6}	***
Habitat type (HT)	1	410.3	410.3	96.111	$< 2 \times 10^{-16}$	***
Depth zone (DZ)	1	2.8	2.8	0.650	0.421	
Season (S)	1	6.6	6.6	1.550	0.214	
Two-way comparisons						
PZ:HT	3	46.1	15.4	3.599	0.0140	*
PZ:DZ	3	1.1	0.4	0.087	0.967	
HT:DZ	1	0.0	0.0	0.011	0.918	
PZ:S	3	53.8	17.9	4.200	6.25×10^{-3}	**
HT:S	1	8.2	8.2	1.926	0.166	
DZ:S	1	7.9	7.9	1.859	0.174	
Three-way comparisons						
PZ:HT:DZ	3	25.2	8.4	1.967	0.119	
PZ:HT:S	3	8.8	2.9	0.690	0.559	
PZ:DZ:S	3	2.6	0.9	0.204	0.893	
HT:DZ:S	1	2.3	2.3	0.540	0.463	
Four-way comparison						
PZ:HT:DZ:S	2	2.5	1.2	0.288	0.750	
Residuals	279	1 268.0	4.3			
Significance key:	"***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1	

2.4.3 Comparison of ichthyofaunal community structures among BRUV deployment sites in the GMPA

Each of the 328 successful BRUV deployment sites in relation to one another based on their ichthyofaunal community structure (Figure 15). The sites are divided into two clusters based on habitat type. The reef and sand habitat type clusters both have similar vertical distributions, but the sand cluster has a wider lateral distribution. There is a clear distinction between the centroid of each habitat type cluster, however, a large amount of site overlap exists.

Both habitat type cluster centroids are located in the 24-26 m depth bracket. The largest concentration of reef and sand sites exist in the 18-26 m and 10-26 m brackets, respectively. Both habitat type clusters have similar community structures at their upper depth limits, but there are more sand-based communities at shallower depths.

Protection zone ellipses were not overlaid as they decreased the interpretability of the ordination plot, but there is a high association between the reef cluster and exploited zones, and the sand cluster and protected zones.

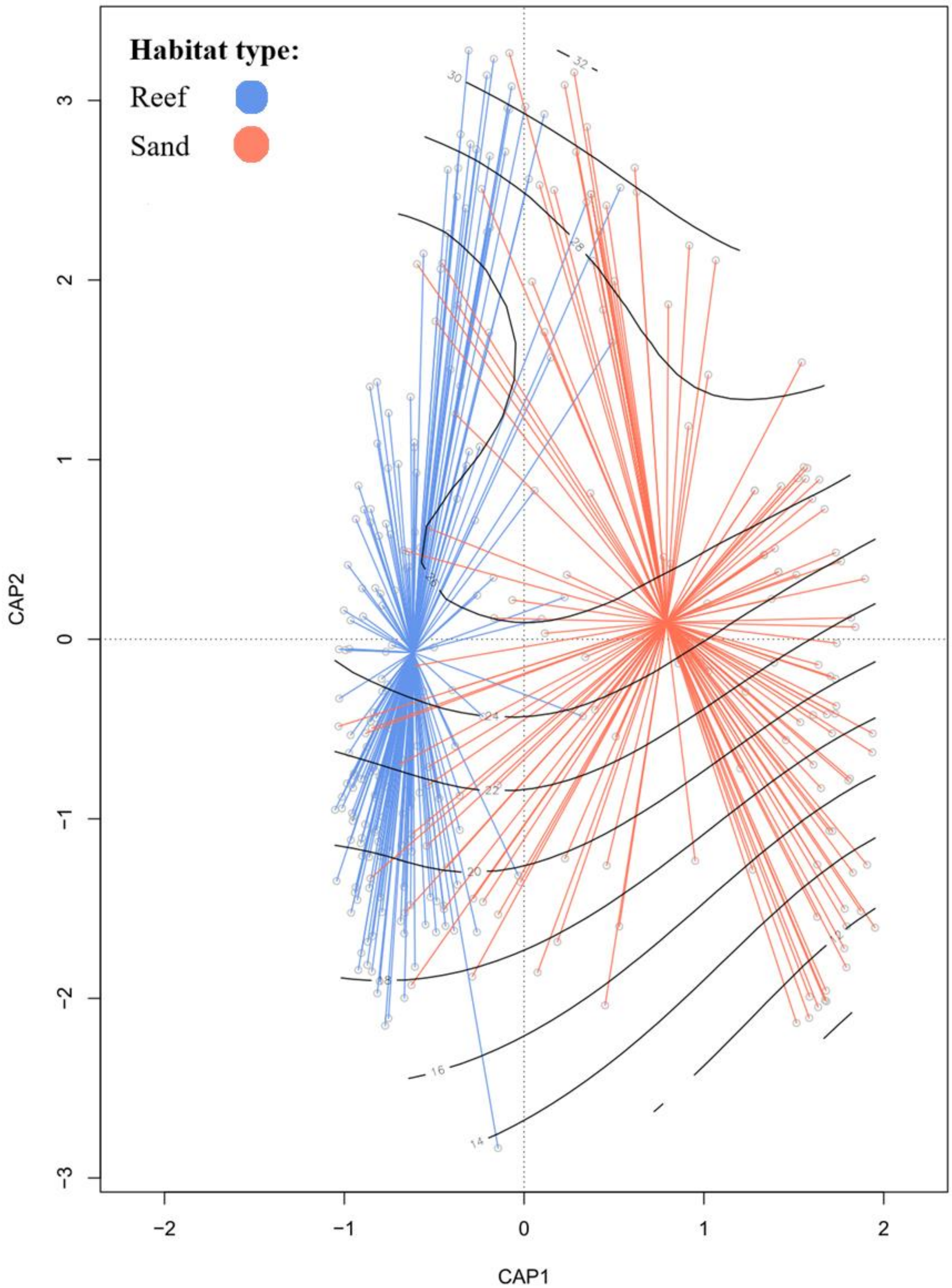

Figure 15: CAP ordination plot of the ichthyofaunal community structures observed at 328 BRUV deployment sites in and around the GMPA over a five-year period (2013-2017). Predictor variables considered were depth (see contour lines), habitat (see legend), and protection status (not shown).

2.4.4 Fish community types in and around the Goukamma MPA

Hierarchical clustering was used to separate each of the 74 fish species recorded by the BRUVs into four groups based on their observed frequencies and relative abundances across the 328 deployment sites at a cut-off level of 1.5 (Table 10 and Figure 16).

Group 1

Group 1 was comprised of 24 species from seven families. The most prominently represented species were sparids (50%), chondrichthyans (17%), and cheilodactylids (13%). All of the chondrichthyans in the group were sharks. All 24 species favoured reef. The majority of the species in the group favoured summer in deep, exploited zones. The group was more prevalent in the NNTZ than the EZ.

Group 2

Group 2 was comprised of 12 species from 10 families. The most prominently represented species were chondrichthyans (75%), of which the majority were skates and rays. Species in the group favoured summer in protected zones over sandy substrata and did not have a depth zone preference.

Group 3

Group 3 was comprised of four species from three families. The most prominently represented species were carangids (50%). The only chondrichthyan in the group was a shark. All four species favoured summer in shallow, protected zones. The majority of the species in the group favoured sandy substrata.

Group 4

Group 4 was comprised of 34 species from 27 families. The most prominently represented species were chondrichthyans (38%), sparids (18%), and sciaenids (9%). Group 4 had the most chondrichthyans, of which 77% were sharks, and the remainder were skates, rays, and a chimaera. The majority of the species in the group favoured summer in deep, protected zones over sandy substrata.

Table 10: Species groupings based on hierarchical analysis.

Species	Family	Species	Family
Group 1		**Group 3**	
Galeichthys ater	Ariidae	*Seriola lalandi*	Carangidae
Chaetodon marleyi	Chaetodontidae	*Trachurus trachurus*	Carangidae
Cheilodactylus fasciatus	Cheilodactylidae	*Carcharhinus brachyurus*	Carcharhinidae
Cheilodactylus pixi	Cheilodactylidae	*Pomadasys olivaceus*	Haemulidae
Chirodactylus brachydactylus	Cheilodactylidae	**Group 4**	
Oplegnathus conwayi	Oplegnathidae	*Callorhinchus capensis*	Callorhinchidae
Haploblepharus edwardsii	Scyliorhinidae	*Lichia amia*	Carangidae
Haploblepharus fuscus	Scyliorhinidae	*Carcharhinus obscurus*	Carcharhinidae
Poroderma africanum	Scyliorhinidae	*Chirodactylus grandis*	Cheilodactylidae
Poroderma pantherinum	Scyliorhinidae	*Clinus superciliosus*	Clinidae
Acanthistius sebastoides	Serranidae	*Dasyatis chrysonota*	Dasyatidae
Epinephelus marginatus	Serranidae	*Dichistius capensis*	Dichistiidae
Boopsoidea inornata	Sparidae	*Gymnura natalensis*	Gymnuridae
Cheimerius nufar	Sparidae	*Pomadasys striatus*	Haemulidae
Chrysoblephus cristiceps	Sparidae	*Notorynchus cepedianus*	Hexanchidae
Chrysoblephus gibbiceps	Sparidae	*Carcharodon carcharias*	Lamnidae
Chrysoblephus laticeps	Sparidae	*Eptatretus hexatrema*	Myxinidae
Diplodus capensis	Sparidae	*Narke capensis*	Narkidae
Diplodus hottentotus	Sparidae	*Carcharias taurus*	Odontaspididae
Gymnocrotaphus curvidens	Sparidae	*Parascorpis typus*	Parascorpididae
Pachymetopon aeneum	Sparidae	*Pomatomus saltatrix*	Pomatomidae
Petrus rupestris	Sparidae	*Raja straeleni*	Rajidae
Pterogymnus laniarius	Sparidae	*Argyrosomus japonicus*	Sciaenidae
Spondyliosoma emarginatum	Sparidae	*Atractoscion aequidens*	Sciaenidae
Group 2		*Umbrina robinsoni*	Sciaenidae
Galeichthys feliceps	Ariidae	*Scyliorhinus capensis*	Scyliorhinidae
Bathytoshia brevicaudata	Dasyatidae	*Serranus cabrilla*	Serranidae
Myliobatis aquila	Myliobatidae	*Cymatoceps nasutus*	Sparidae
Rostroraja alba	Rajidae	*Lithognathus mormyrus*	Sparidae
Acroteriobatus annulatus	Rhinobatidae	*Pachymetopon grande*	Sparidae
Halaelurus natalensis	Scyliorhinidae	*Polysteganus undulosus*	Sparidae
Pagellus natalensis	Sparidae	*Rhabdosargus holubi*	Sparidae
Squalus megalops	Squalidae	*Sarpa salpa*	Sparidae
Amblyrhynchotes honckenii	Tetraodontidae	*Sphyrna zygaena*	Sphyrnidae
Mustelus mustelus	Triakidae	*Lagocephalus sceleratus*	Tetraodontidae
Mustelus palumbes	Triakidae	*Torpedo fuscomaculata*	Torpedinidae
Triakis megalopterus	Triakidae	*Galeorhinus galeus*	Triakidae
		Chelidonichthys kumu	Triglidae
		Cremnochorites capensis	Tripterygiidae

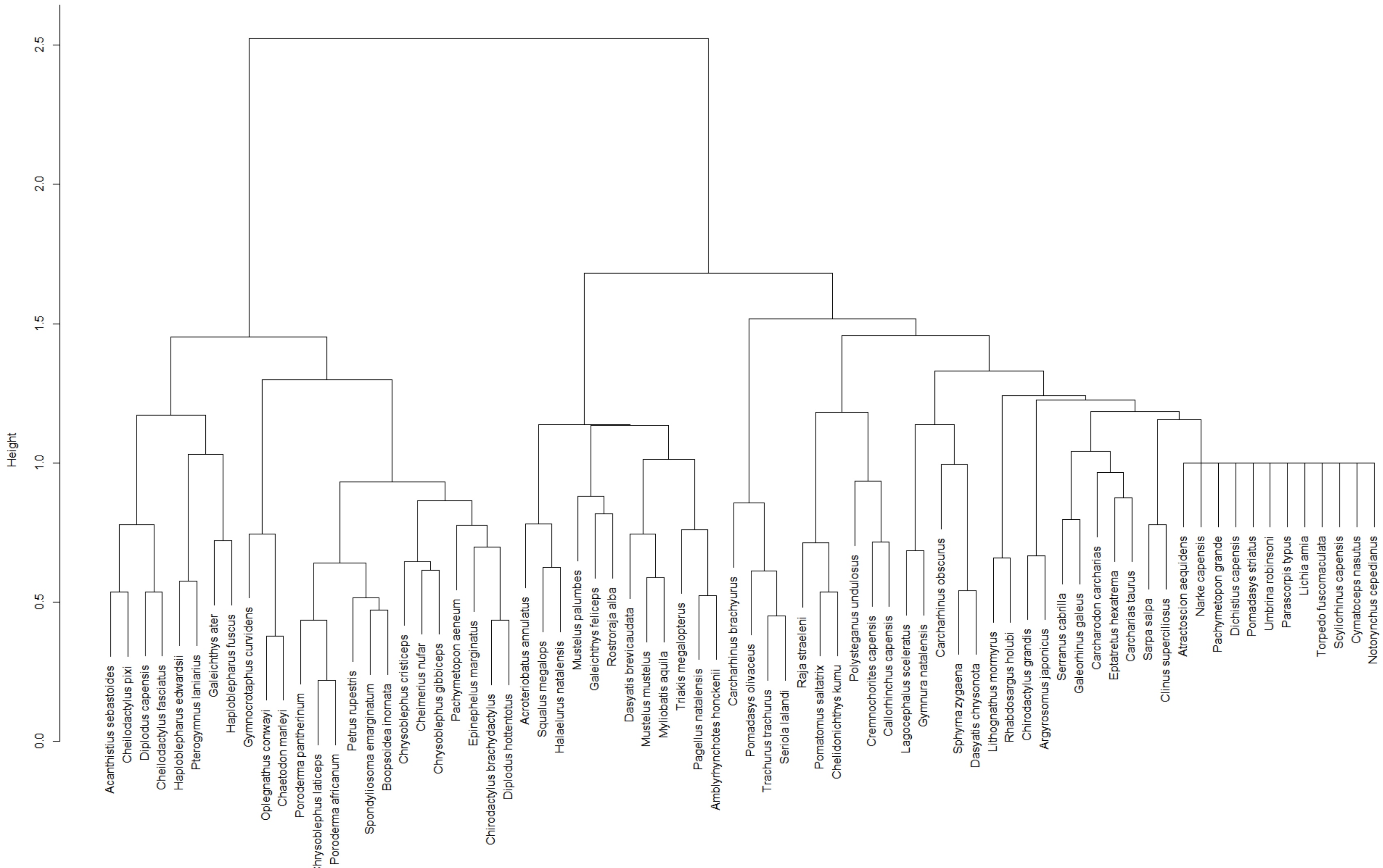

Figure 16: A dendrogram of species groups based on 328 BRUV deployments in Goukamma at a cut-off level of 1.5.

2.4.5 Comparison of BRUV data to CPUE and UVC data

Four previous ichthyofaunal surveys have been conducted in Goukamma's surf and shallow subtidal zones between 2000 and 2011 (Götz, 2005; Pradervand & Hiseman, 2006; Götz et al., 2009b; Attwood et al., 2016). The surveys made use of a mixture of CAS, roving creel, and UVC methods.

In total, the BRUVs recorded 51% more fish species than CAS and 61% more than UVC. Overall relative abundances were 76% higher than in CAS and 30% higher than in UVC. All three data sets were recorded over the course of five years and each found the four most common species in and around the GMPA to be *B. inornata*, *C. laticeps*, *P. aeneum*, and *S. emarginatum*. A similar inshore CAS and UVC survey was conducted in 2005 as part of an assessment of Goukamma's effect on community structure and fishery dynamics and identified the same four dominant species (277 CAS sites and 177 UVC point counts) (Götz, 2005).

A boat-based survey conducted in and around the MPA produced 273 CAS and 44 UVC point counts over a five-year period between 2000 and 2004 (Götz et al., 2009b). The CAS found the most commonly caught species to be sparids and the UVC point counts corroborated this. A comparison of the CAS and UVC data to BRUV data collected in the same zones indicated that the BRUVs recorded the same amount of sparid species as CAS and 11% more than UVC. The relative abundance of sparids recorded by the BRUVs was 69% higher than in the CAS and 11% higher than in the UVC. The BRUVs also recorded 67% more chondrichthyan species than CAS and 89% more than UVC. The relative abundance of chondrichthyans recorded by the BRUVs was 95% higher than that recorded by CAS and 99% higher than that recorded by UVC (Table 11).

Shore-based CAS and roving creel surveys conducted in Goukamma in 2006, 2009, and 2011 found the most commonly caught species to be *Dichistius capensis*, *Diplodus capensis*, and *S. salpa* (Pradervand & Hiseman, 2006; Attwood et al., 2016). These results differ completely to those observed on the BRUVs where *B. inornata*, *C. laticeps*, and *S. emarginatum* dominated, however, it is important to note that the shore-based survey targeted Goukamma's surf zone (0-5 m) as opposed to the shallow subtidal zone (5-45 m). This is a good example of how BRUV and CAS can be used to complement one another when monitoring a marine area with multiple habitats.

Table 11: Comparison of 648 BRUV, CAS, and UVC samples from Goukamma's surf zone and inshore waters (< 45 m) (273, 331, and 44 samples respectively).

Species	Relative abundance		
	BRUV	**CAS**	**UVC**
	Sparids		
Argyrozona argyrozona	0	0.0015	0
Boopsoidea inornata	1.9769	1.0602	3.8565
Cheimerius nufar	0.5386	0.1281	0.0772
Chrysoblephus cristiceps	0.1343	0.0648	0
Chrysoblephus gibbiceps	0.1343	0.0185	0.0293
Chrysoblephus laticeps	1.625	1.6806	0.7654
Cymatoceps nasutus	0.0015	0.0015	0.0015
Diplodus capensis	0.3148	0.0139	0.25
Diplodus hottentotus	0.1836	0.0031	0.1914
Gymnocrotaphus curvidens	0.0417	0.0031	0.1296
Lithognathus mormyrus	0.0586	0	0.0046
Pachymetopon aeneum	0.7654	0.1373	1.3318
Pachymetopon blochii	0	0.0015	0.0046
Pachymetopon grande	0.0123	0.0046	0.0216
Pagellus natalensis	0.4522	0.0725	0
Petrus rupestris	0.0926	0.0139	0.0231
Polysteganus undulosus	0.0077	0	0
Pterogymnus laniarius	0.2392	0.017	0.0015
Rhabdosargus holubi	0.0046	0.0015	0
Sarpa salpa	0.196	0.0046	0.7083
Sparodon durbanensis	0	0	0.0046
Spondyliosoma emarginatum	4.6636	0.3102	3.1991
	Chondrichthyans		
Acroteriobatus annulatus	0.0247	0	0
Callorhinchus capensis	0.0062	0	0
Carcharhinus brachyurus	0.0216	0.0015	0
Carcharhinus obscurus	0.0262	0.0031	0
Carcharias taurus	0.0185	0	0.0046
Carcharodon carcharias	0.0077	0	0
Bathytoshia brevicaudata	0.0741	0	0
Dasyatis chrysonota	0.0093	0	0
Galeorhinus galeus	0.0231	0	0
Gymnura natalensis	0.0031	0	0
Halaelurus natalensis	0.0509	0	0
Haploblepharus edwardsii	0.1373	0.0139	0.0015
Haploblepharus fuscus	0.0494	0	0
Mustelus mustelus	0.3256	0.0201	0
Mustelus palumbes	0.0093	0	0
Myliobatis aquila	0.091	0	0
Narke capensis	0.0046	0	0
Notorynchus cepedianus	0.0154	0	0
Poroderma africanum	1.0015	0.0417	0.0031
Poroderma pantherinum	0.2407	0.0231	0
Raja straeleni	0.0062	0	0
Rostroraja alba	0.0278	0	0

Table 11 (continued): Comparison of 648 BRUV, CAS, and UVC samples from Goukamma's surf zone and inshore waters (< 45 m) (273, 331, and 44 samples respectively).

Species	**Relative abundance**		
	BRUV	**CAS**	**UVC**
Chondrichthyans (continued)			
Scyliorhinus capensis	0.0015	0	0
Sphyrna zygaena	0.0231	0.0093	0
Squalus megalops	0.0926	0.0015	0
Torpedo fuscomaculata	0.0031	0	0
Triakis megalopterus	0.0185	0.0031	0
Other			
Acanthistius sebastoides	0.0941	0.0448	0.0031
Amblyrhynchotes honckenii	0.2685	0	0
Argyrosomus japonicus	0.0031	0	0
Atractoscion aequidens	0.0123	0.0093	0
Chaetodon marleyi	0.0278	0	0.017
Cheilodactylus fasciatus	0.0417	0	0.034
Cheilodactylus pixi	0.0787	0	0.0278
Chelidonichthys kumu	0.0062	0	0
Chirodactylus brachydactylus	0.1929	0	0.2963
Chirodactylus grandis	0.0062	0	0
Clinus superciliosus	0.0015	0	0
Cremnochorites capensis	0.0046	0	0
Dichistius capensis	0.0015	0	0.0031
Epinephelus marginatus	0.0509	0	0
Eptatretus hexatrema	0.0062	0	0
Galeichthys ater	0.1914	0	0
Galeichthys feliceps	0.2963	0.0633	0
Lagocephalus sceleratus	0.0046	0	0
Lichia amia	0.0015	0	0
Oplegnathus conwayi	0.1235	0	0.2886
Parascorpis typus	0.0031	0.0015	0.0123
Pomadasys olivaceus	0.2083	0.0278	0.1481
Pomadasys striatus	0.0015	0	0
Pomatomus saltatrix	0.6404	0.0031	0
Scomber japonicus	0	0.0247	0
Seriola lalandi	0.0617	0	0
Serranus cabrilla	0.0154	0	0
Trachurus trachurus	0.2022	0.0031	0
Umbrina robinsoni	0.0015	0	0

2.5 Discussion

At 328 successful samples over the course of a five-year period, this study presents one of the largest and longest-running BRUV data set collected along South Africa's south coast to date. Despite the 2017 survey being cut short, data continues to be collected in Goukamma and will represent a ten-year data set by the end of 2022. Long-term biological data sets are essential to understanding population biology in marine systems as they allow us to document ecosystem changes and differentiate between natural change and change driven by anthropogenic stressors (Wolfe et al., 1987).

Whilst bi-annual surveys of Goukamma were unfeasible, a solution could be to lower the deployment target to 30-35 BRUVs per season and revert to conducting the survey biannually. This would allow for a more diverse data set as well as increased flexibility for the GMPA's limited staff. It would result in lower species richness and relative abundance counts for each season but would allow for a higher degree of comparability on an annual basis and potentially help to highlight seasonal migratory tendencies in certain species as well as the effects of increased upwelling in the summer. It would also likely increase the overall recorded species diversity in and around the GMPA as there would be a higher representation of winter-associated species

There was a partial bias towards deployments over deep, rocky reefs in protected zones. It is not uncommon for there to be a bias towards rocky reefs and protected zones in ichthyological surveys along South Africa's south coast, as they are expected to harbour higher concentrations of fish than sandy substrata and exploited zones (De Vos et al., 2014; Roberson et al., 2015; Parker et al., 2016b). This could be mitigated in future surveys by adjusting the survey design to randomly select eight reef sites and eight sand sites in each of the protection zones instead of just 16 random sites per zone.

2.5.1 Differences in species composition among the GMPA's proposed and pre-existing zones

Multi-factor ANOVA and non-parametric Kruskal-Wallis tests identified significant differences between the species richness, abundance, and diversity of Goukamma's four protection zones. Post hoc Tukey and Dunn's test confirmed that the NNTZ had a significantly higher diversity and abundance of fish than the NEZ. This confirms that differences in species composition exist among the GMPA's proposed and pre-existing zones and that there are more reef fish in the NNTZ than the NEZ.

C. cristiceps, *C. gibbiceps*, *P. rupestris*, and *P. undulosus*, are all endangered and favoured the EZ and NNTZ (Buxton et al., 2014; Mann et al., 2014e,j,k). Götz et al.'s (2009a) proposed swap in protection status of the NNTZ and NEZ would lead to increased protection of these endangered sparids and an overall higher diversity of species being protected by the GMPA.

2.5.2 The effects of physical and environmental variables on species composition and abundance across Goukamma's protection zones

Multi-factor ANOVA and non-parametric Wilcoxon signed-rank tests identified habitat type as the most significant determinant of species richness, abundance, and overall evenness in and around the GMPA. CAP ordination was used to visually interpret differences in community structure between the habitat types by creating a reef and a sand cluster. Distinction between reef and sand sites was based upon the most predominant habitat type in the FOV of each BRUVs' deployment and overlap in between the middle of the two habitat clusters is likely indicative of similarity in community structures as a result of mixed habitat types (i.e. sand sites in close proximity to reef).

Several of the sand sites overlap the reef cluster's centroid, which could be the result of BRUVs landing on the boundaries of reef, with the FOVs facing outwards and the sites thus being classified as sandy substrata. In these cases, the community structures of these reef-adjacent sand sites would be strongly influenced by reef-associated species. None of the reef sites extend past the sand centroid, which is indicative that the majority of the central overlap likely stems from mixed habitat-based community structures. The overlapping sites in between the two habitat clusters' centroids should be individually reviewed with UVC, further BRUV deployments, or against bathymetric maps to more effectively determine their habitat types and whether the case for a mixed habitat classification needs to be made. The community structures of reef and sand sites are distinctively different near the lower depth limits.

Protection zone was a similarly significant determinant in the significance models and on the ordination plot. The high association between the reef cluster and exploited zones and the sand cluster and protected zones further emphasised the imbalance in the zonation of the two habitat types in the GMPA. The EZ and NNTZ had the most diverse community structures of the four protection zones. These zones are located on the western and seaward boundaries of the MPA along the subtidal reef identified by Götz et al. (2009a). Despite being open to fishing, the higher prevalence of reef in the two exploited zones likely played a role in inflating their species richness and abundance above that of the sand-dominated protected zones through higher concentrations of sparids and other reef-associated species.

The higher species diversity in the exploited zones might also be indicative of the early signs of serial overfishing (Soh et al., 2001). Dominant predator species such as *C. laticeps* are targeted by anglers, which lowers their top-down impact on the remainder of the ecosystem (Bianchi et al., 2000; Götz et al., 2009b). Higher pressure on predator species alleviates pressure on prey species, allowing more of juveniles to reach recruitment (Ashworth & Ormond, 2005; Frank et al., 2005). The scenario that unfolds when predators are removed is often equivalent to that of an inverse J-curve (Panayotou, 1997): there is an initial rise in species richness and abundance as prey species thrive in the absence of predation, whereafter select unchecked prey species might outcompete the others and become dominant. The resulting trophic cascade can lead to a drastic decrease in overall species richness (Pace et al., 1999). A potential buffer to the effects of serial overfishing and trophic cascades in Goukamma's exploited zones is the comparatively high complexity of their reefs (deduced from sites' contour profiles), which has been shown to lessen the impact of these phenomena in other reef systems (Grabowski, 2004), as well as spillover from its protected zones (Kerwath et al. 2013).

Despite favouring rocky reefs over sandy substrata, sparids were still one of the main components of sand-based community structures throughout the survey. It can be assumed that the western section of the MPA's sandy substrata that was not sampled during the survey had similar species compositions to those observed in the NTZ. These communities are well represented in the NTZ and should not be negatively affected by the opening of the NEZ to fishing. On the contrary, the protection of the NNTZ might act as a buffer to the sand-based communities, as anglers would no longer be able to fish along the NTZ's seaward boundary. Predators in both the reef- and sand-associated communities would potentially benefit from the spillover of sparids and other prey species from the NNTZ should its protection result in increased recruitment, which is likely considering its bathymetric potential to be a rocky nursery area.

Depth zone was a significant determinant of species richness but not abundance or overall evenness. Season did not significantly affect community structure in and around the GMPA. Seasonal changes in fish assemblages are well documented and are often attributed to migratory behaviour, such as juveniles reaching recruitment and shifting from nursery grounds to areas more suited to feeding and spawning (Rooker & Dennis, 1991; Hyndes et al., 1999; Ribeiro et al., 2006; Barletta et al., 2008; Espírito-Santo et al., 2009). The lack of a significant difference in community structure between summer and winter is potentially indicative of a high degree of residency amongst Goukamma's fish species.

The most abundant species, *B. inornata*, *C. laticeps*, and *S. emarginatum*, inhabit rocky reefs between 5-30 m (Penrith, 1972a), with juveniles favouring shallow subtidal rocky substrata over estuaries and mangroves (Penrith, 1972b; Buxton & Smale, 1984; Mann et al., 2014a,c,d). Goukamma's offshore reefs and the Walker's Point cluster are potential spawning areas for these species. All three sparids spawn in spring and summer (Buxton & Smale, 1984; Götz, 2005; Fairhurst et al., 2007) and display residential behaviour (Penrith, 1972a; Kerwath et al., 2007a; Tunley et al., 2009; Mann et al., 2014a,c; Ensair, 2019).

The most abundant scyliorhinids, *H. edwardsii*, *P. africanum*, and *P. pantherinum*, are predominantly benthic-dwelling organisms and are generally not strong swimmers (Grusd et al., 2019). Both *H. edwardsii* and *P. africanum* have been observed maintaining small territorial ranges (Dainty, 2002; Escobar-Porras, 2009; Human, 2009a), and all three species favour rocky reefs over sandy habitats in shallow subtidal environments (Compagno, 2009c; Human, 2009a,b). None of these scyliorhinids have been observed to conform to specific breeding seasons (Dainty, 2002; Compagno, 2009c). Chondrichthyans tend to be relatively more mobile than reef-reliant species like sparids, with subsequently expansive geographic distributions and migratory tendencies (Compagno et al., 1991). This is not the case for all chondrichthyans, however, as evidenced by the residency of the scyliorhinids, which has been shown through tagging during CAS (Escobar-Porras, 2009).

Whilst overall species richness was not significantly affected by season, more species were observed in the shallow zone during summer than winter, which is indicative of recruitment of smaller fish into the shallow zone during summer or that the majority of the fish are not leaving the MPA and surrounding waters but are potentially shifting their feeding ranges seasonally. Upwelling along South Africa's temperate south coast is more prevalent in summer and autumn than winter and spring (Schumann et al., 1982). Increased upwelling during the summer season would result in surplus nutrients in shallower waters, which could in turn play a role in the observed higher species richness in the shallow zone during summer. Sparids on the south coast have been observed to shift their distributions as a result of cold upwelling, which is another potential reason for the increased species richness in the shallow zone during summer upwelling months (Buxton & Smale, 1989). The stability of Goukamma's species richness irrespective of season can likely be explained by the fact that almost 80% of the fish species appear to be residential.

2.5.3 Fish community types in Goukamma

Four community groups were identified in Goukamma using hierarchical clustering. A relatively low cophenetic correlation coefficient of 0.25 can be explained by the massive overlap in species assemblage observed throughout the study. The groups represent species that are likely to be found at the same sites. Of the four groups, only the first was predominantly associated with the reef and exploited zones. Species in the group specifically favoured the NNTZ. Half of the group was made up of sparids, which included commercially and recreationally important species like *C. laticeps* (Lamberth & Joubert, 2014), as well as *C. cristiceps*, *C. gibbiceps* and *P. rupestris*, which are endangered endemics (Smale, 1988; Van Zyl, 2013; Buxton et al., 2014). The sharks in the group were all scyliorhinids, which have a similar feeding niche to the sparids (Penrith, 1972a; Ebert et al., 1996).

The second group was a sand-based community dominated by skates, rays, and triakids. The only sparid in the group was *P. natalensis*, a sand-associated species which is potentially preyed upon by the chondrichthyans (Mann et al., 2014i). The ariid *G. feliceps* and the tetraodontid *A. honckenii* are likely not frequently predated upon. The sharks in the group predominantly feed on benthic crustaceans (Ebert et al., 1996; Smale & Compagno, 1997).

The third group was the smallest of the four and represented a potential predation interaction. The group was made up of two carangids, a carcharhinid, and a haemulid. The carangids, *S. lalandi* and *T. trachurus*, both prey upon smaller fish and potentially target the haemulid, *P. olivaceus*, in its juvenile stages (Binohlan & Capuli, 2019; Luna & Bailly, 2019a,b). The remains of all three of these species have been found in the stomach contents of carcharhinid *C. brachyurus* (Smale, 1991; Cliff and Dudley, 1992). The presence of *P. olivaceus* potentially attracts the carangids, and together the three species potentially attract *C. brachyurus*.

The fourth group was the largest of the four and was made up of several species of chondrichthyans, sand-associated sparids, and sciaenids. The critically endangered sparid *P. undulosus* was identified as part of this group (Mann et al., 2014e). The groups' chondrichthyans represented several of the apex predators in and around the GMPA and included *C. carcharias*, *C. obscurus*, *G. galeus*, *M. mustelus*, and *T. megalops*. It also included two of the most predominant scyliorhinids in the study, *P. africanum* and *P. pantherinum*. Potential prey species included the sciaenids and sparids.

2.5.4 BRUV as a viable replacement for CAS and UVC surveys

No single survey method is perfect, as all have biases which will either over- or under-represent certain species. The BRUV survey recorded higher overall percentages of fish species and relative abundance than the CAS and UVC survey in and around the GMPA. Chondrichthyans were especially well represented in the BRUV survey as opposed to the CAS and UVC survey. The UVC survey recorded a similar number of sparid species to the BRUV survey but a lower relative abundance.

Goukamma's surf zone is dominated by *Dichistius capensis*, *Diplodus capensis*, and *S. salpa* (Pradervand & Hiseman, 2006; Attwood et al., 2016). *Dichistius capensis* is a surf zone species and *S. salpa* are migrant herbivores that feed on algae in shallow water (Russell et al., 2014; Hall, 2015; Binohlan & Sampang-Reyes, 2019), making them less likely to be observed by the deeper subtidal BRUVs and more likely to be caught by shore-based anglers. *Diplodus capensis* is an omnivore that feeds on a wide variety of organisms and inhabits rocky reefs down to 40 m (Mann et al., 2014b), making it a likely candidate to feature in shore-based CAS and BRUV surveys. It was however underrepresented in the shallow subtidal BRUV survey when compared to other sparids such as *B. inornata*, *C. laticeps*, and *S. emarginatum*, which were in turn underrepresented in the surf zone CAS (Pradervand & Hiseman, 2006). All three of these sparids are benthic carnivores/omnivores (Mann et al., 2014a,c,d), and are thus likely to be attracted to the bait cannisters deployed in the subtidal zone. *U. ronchus*, which was recorded in the CAS but not on the BRUVs, was misidentified and was actually *U. robinsoni*, which is more likely to be found in the surf zone and was observed during the BRUV survey (Hutchings & Griffiths, 2005).

Goukamma's subtidal zone is dominated by *B. inornata*, *C. laticeps*, and *S. emarginatum* (Götz, 2005; Götz et al., 2009b). BRUV, CAS, and UVC all produced similar data with regard to the most prominent species in this zone. Both *B. inornata* and *S. emarginatum* were underrepresented in the CAS as compared to the BRUVs and UVC surveys, whereas *C. laticeps* was underrepresented in the UVC survey as compared to the CAS and BRUV survey. This was likely a result of bait attraction.

CHAPTER 3: A comparison of the ichthyofaunal community structures of the Betty’s Bay, Goukamma, Stilbaai, and Tsitsikamma Marine Protected Areas

3.1 Abstract

BRUV data from Betty’s Bay, Stilbaai, and Tsitsikamma were available for comparison with the Goukamma data. The four study areas are spaced out over 500 km of coastline, which allowed for an extensive analysis of ichthyofaunal community structures along the warm-temperate south coast. The objective of this analysis was to measure complementarity and redundancy of protection among the south coast’s MPAs. High redundancy of protection is a good measure of an area’s overall level of ichthyofaunal protection. A combined MPA data frame of 466 successful BRUV deployments was created from the four MPAs’ data. Fish assemblages among the study areas were tested with permutational multivariate analysis of variance tests, similarity of percentages tests, and canonical analysis of principal coordinates. Complementarity and/or redundancy among the MPAs studied was tested using multilevel patterns analyses. Goukamma had the highest species richness and diversity, followed by Tsitsikamma, Betty’s Bay, and Stilbaai. PERMANOVA tests indicated that study area ($F = 27.1$, $P = 1.00 \times 10^{3}$), depth zone ($F = 17.4$, $P = 1.00 \times 10^{3}$), and habitat type ($F = 91.8$, $P = 1.00 \times 10^{3}$) were all significant factors in determining community structure. Habitat type was the most significant determinant of community structure along the south coast and needs to be appropriately accounted for in MPA spatial planning so as to avoid potentially ineffective protected zones, as seen in Goukamma. Reef sites had higher species richness and abundance than sand sites. Betty’s Bay had the most unique community structure and lowest redundancy of protection among the four study areas as the result of localised kelp forests, which were absent in the other three study areas. Species richness was lower on the western side of the south coast than the eastern side, which supports the concept of subtropical subtraction. Seventy (79%) of the 88 species recorded among the study areas were represented in two or more of the four MPAs. Goukamma had the highest number of unique species records, and offered the highest complementarity for chondrichthyans, whereas Betty’s Bay’s offered the highest complementarity for reef- and kelp-associated species. This is a good indication that shallow subtidal fish communities are well protected along South Africa’s south coast.

3.2 Introduction

South Africa was ranked 30th in the world for marine protection in 2018 (UNEP-WCMC & IUCN, 2020), based on the percentage of its territorial waters which are formally protected by MPAs. This ranking took place prior to the implementation of the Operation Phakisa MPA network, which has increased South Africa's national protection by 93% (Sink et al., 2019). South Africa's 41 national MPAs vary in size and spacing, ranging from coastal MPAs as small as 1.5 km^2 to offshore MPAs as large as 10 700 km^2 (Sink et al., 2019; UNEP-WCMC & IUCN, 2020). The relative size and spacing of MPAs has a strong effect on their conservation efficacy (Moffitt et al., 2011). There are numerous MPAs spaced out along the south coast, which have the potential to complement one another and offer redundancy in protection, as well as supplement exploitable fishing grounds through the spillover of adult fish, eggs, and/or larvae (McClanahan & Manga, 2000; Ashworth & Ormond, 2005).

The south coast of South Africa represents a unique marine biogeographic zone called the Agulhas Biozone. Comparable BRUV data from the Betty's Bay MPA (BBMPA), Goukamma MPA (GMPA), Stilbaai MPA (SMPA), and Tsitsikamma MPA (TMPA) present a good opportunity to describe their total species coverage, complementarity, and redundancy. Unfortunately, BRUV data from the De Hoop MPA, located in between the BBMPA and SMPA (Figure 17), were not available at the time of this study.

Objectives of this chapter included a comparison of the ichthyofaunal abundance and community structures of Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma, an analysis of species' associations with physical and environmental variables among the study areas, and a review of subtropical subtraction and MPA complementarity/redundancy along the south coast.

A review of the Betty's Bay, Stilbaai, and Tsitsikamma MPAs

BRUV data collected Betty's Bay (Roberson et al., 2015), Stilbaai (De Vos et al., 2014), and Tsitsikamma (Bernard et al., 2014) were compared to the Goukamma BRUV data for a description of coastal ichthyofaunal communities along South Africa's warm-temperate south coast. The four study areas are spread out across a stretch of approximately 500 km of the south coast, starting with Betty's Bay on the western extreme, Stilbaai and Goukamma in the middle, and Tsitsikamma on the eastern extreme (Figure 17). They are all managed by the Western Cape Nature Conservation Board (CapeNature), except for Tsitsikamma, which is managed by

South African National Parks (SANParks). These MPAs collectively protect 266.3 km^2 of South Africa's national waters (Chadwick et al., 2014).

The Betty's Bay MPA

The BBMPA was established in 1981 and is home to the Stony Point African penguin (*Spheniscus demersus*) colony. The MPA forms part of the larger Kogelberg Biosphere Reserve between Gordon's Bay and Hermanus. Despite its relatively small size, the BBMPA protects a large variety of habitats including an estuary, kelp forests, rocky shores, sandy beaches, and subtidal reefs (Tunley, 2009).

Controlled shore-based angling is permitted in the MPA, however, a BRUV survey conducted in 2015 found no significant difference in species composition between the protected and exploited zones, which might be an indicator of poor enforcement of regulations in Betty's Bay (Roberson et al., 2015). Staff shortages were noted in the 2009 *State of Management of South African MPAs* (SOMSAMPA) report, which prevented the effective mitigation of abalone poaching in the MPA (Tunley, 2009).

The BBMPA is the second smallest of the four MPAs, with a total size of 20.1 km^2 (Figure 18). It is the only MPA in the group that supports kelp forests alongside the rocky reefs and sandy substrata that dominate the south coast's benthic environment.

The Stilbaai MPA

The SMPA was established in 2008 and includes the Goukou River Estuary, which is permanently open and contains a nursery area for coastal fish (Tunley, 2009). The MPA is separated into three no-take zones and a controlled angling area between the estuary mouth and ocean, with the goal of providing protection for several species of reef fish, sharks, and southern right whales (*Eubalaena australis*).

Stilbaai is one of two places left in South Africa where traditional stonewall fish traps, known as vywers, still exist (Tunley, 2009). Whilst historically and culturally important, the vywers present a dilemma for the MPA's management, as their continued use ensures their maintenance but also poses a risk to the sustainability of local fish populations. Large numbers of *A. japonicus*, *Dichistius capensis*, *P. saltatrix*, white musselcracker (*Sparodon durbanensis*), and white steenbras (*Lithognathus lithognathus*) have been recorded in vywer catches (Kemp et al., 2009). The 2009 SOMSAMPA report noted that an adequate number of staff were available to patrol and enforce the MPA's regulations (Tunley, 2009).

The SMPA is the smallest MPA in the group, although it is only fractionally smaller than the BBMPA, with a total size of 20 km^2 (Figure 18). Its benthos is comprised of rocky reefs and sandy substrata.

The Tsitsikamma MPA

The TMPA was established in 1964 and spans 60 km of the Garden Route, effectively conserving 11% of South Africa's warm-temperate south coast's rocky shoreline (Götz et al., 2008). This stretch of coast is estimated to attract over 170 000 people per annum (Tunley, 2009). The area features several boulder bays and the marine environment consists of a sandy benthos and rocky reefs (Chadwick et al., 2014). The main aims of the MPA are to conserve intertidal bait stocks and mussel beds, as well as nearshore and inshore fish stocks (Cole et al., 2009).

The MPA includes several small estuaries and supports many marine bird species. Over 200 species stemming from 80 families of marine fishes have been recorded in and around Tsitsikamma (Wood et al., 2000; Chadwick et al., 2014), many of which have a high degree of residency (Tunley, 2009). The entire area was originally a no-take zone but significant socio-political pressure over the years resulted in a restructure of its boundaries to incorporate three controlled-angling zones in 2016 (Sunde & Isaacs, 2008; Lombard et al., 2020). Persistent illegal fishing and fertiliser run-off from neighbouring dairy farms pose threats to the MPA, but the 2009 SOMSAMPA report indicated that the enforcement of regulations was being as adequately handled as possible (Tunley, 2009). A UVC survey conducted between 1984 and 1986 found that *C. cristiceps*, *C. laticeps*, and *P. rupestris* were significantly more abundant and on average larger within the MPA than the surrounding waters (Buxton & Smale, 1989).

The TMPA is the largest of the four MPAs, with a total size of 324 km^2 (Figure 18). It is more than four times the size of the other three MPAs combined. Much like the GMPA and SMPA, the TMPA's benthos is predominantly comprised of rocky reefs and sandy substrata.

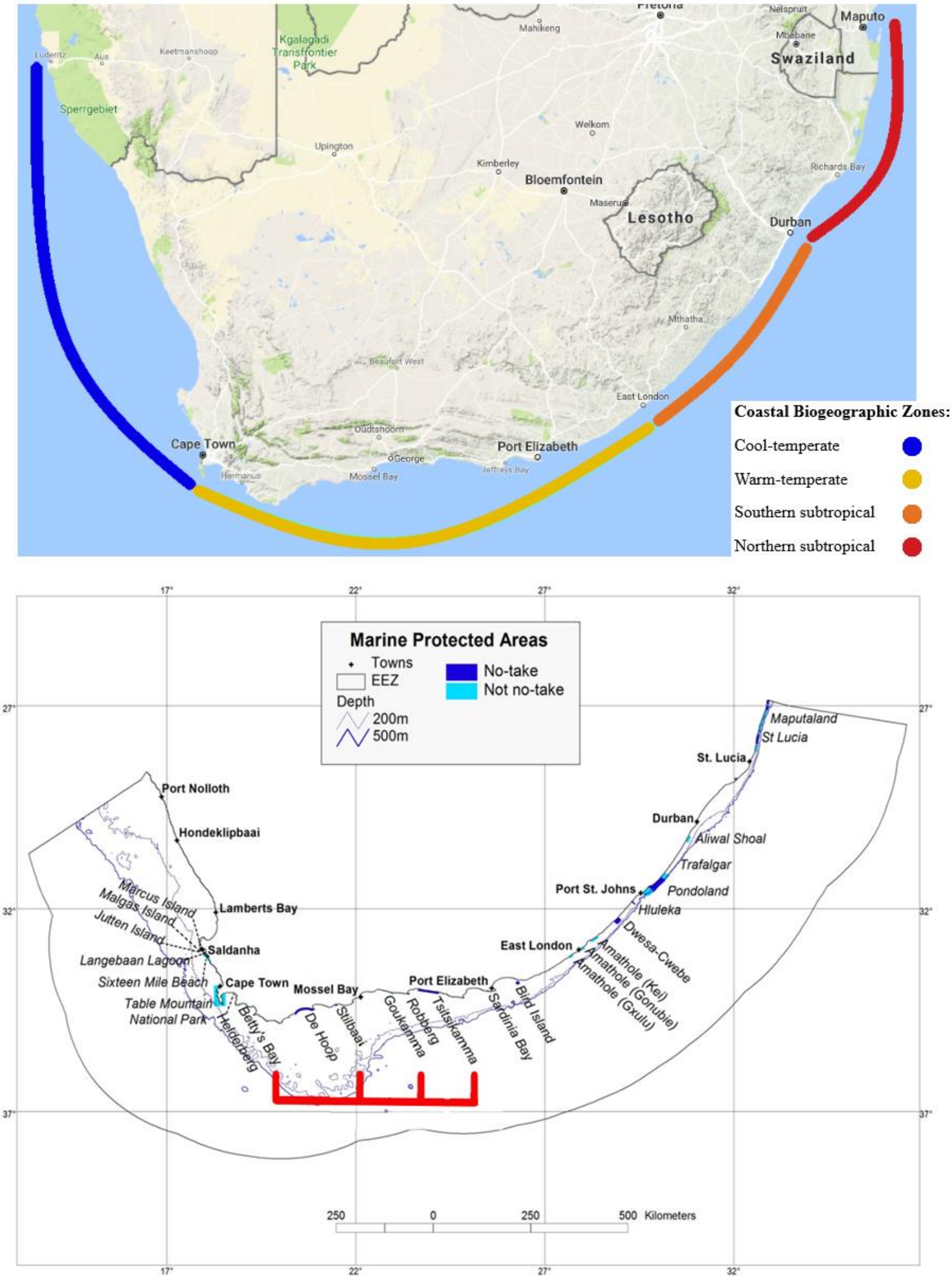

Figure 17: Biogeographical zones and MPA distribution along South Africa's coastline (Operation Phakisa MPAs are not shown). The positions of the Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma MPAs are indicated in relation to the continental shelf. Adapted from the *National Biodiversity Assessment 2011: Technical Report (Volume 4: Marine and Coastal Component)* and Google Maps (van der Elst, 2007; Griffiths et al., 2010; Driver et al., 2012; Spencer et al., 2016).

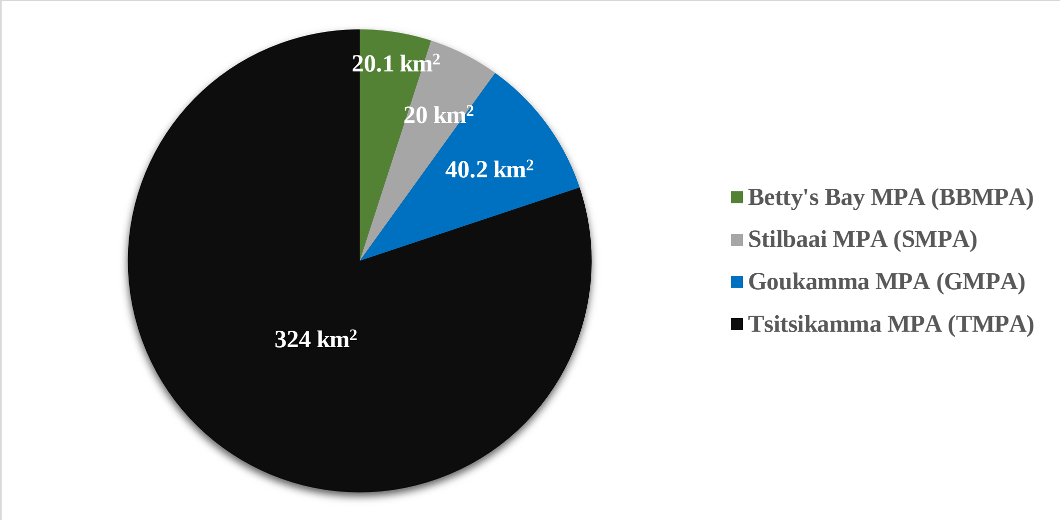

Figure 18: The relative size of the Betty’s Bay, Stilbaai, Goukamma, and Tsitsikamma MPAs (Chadwick et al., 2014).

3.3 Methods

Mono-BRUV data from Betty’s Bay, Stilbaai, Goukamma and Tsitsikamma were combined into a single data frame of 466 successful deployment records. Each record included protection status, depth zone (as defined in Chapter 2), habitat type, and species information (species, common name, family, and MaxN count). The secondary data frame was created with species on the columns and sites on the rows to run multivariate analyses on.

Site-specific habitat type data was not available for Betty’s Bay, however, the habitat ratio was reported to be primarily reef, with just over a third of the area being made up of kelp forests and sandy substrata (Roberson et al., 2015).

3.3.1 Comparing ichthyofaunal assemblages among the MPAs

BRUV data from each of the four study areas were tested to determine whether ichthyofaunal assemblages and species’ associations with physical and environmental variables differed among them, whether species richness and abundance decreased from east to west along the south coast according to subtropical subtraction, and whether the MPAs are complementary or offer redundancy in protection. PERMANOVA tests, similarity of percentages (SIMPER) tests, and CAP ordination were used.

PERMANOVA and SIMPER tests

The effects of area, depth zone, and protection status on the community structure of each of the four area's community structures were tested with a PERMANOVA. No inferences of the effect of protection status could be made because the model was unbalanced with respect to this binary variable, but it was nevertheless important to include this parameter to remove its possible influence on the remaining parameters. Habitat type could not be included in the test as an independent variable, due to the lack of site-specific habitat data from Betty's Bay. The vegdist function (method = "horn"; *vegan v2.4-2*) (Okansen et al., 2018) was used to apply the Morisita-Horn dissimilarity index to the data frame to account for differences in the sizes of the MPAs' data sets (Chao et al., 2006). The adonis function (permutations = 999; *vegan v2.4-2*) (Okansen et al., 2018) was used to perform the PERMANOVA test.

SIMPER tests were used to identify the species which played the largest roles in the dissimilarity among the study areas and depth zones. The species that were considered as playing the largest role were the ones which contributed to the first 50% of each SIMPER test's cumulative sum. The simper function (*vegan v2.4-2*) (Okansen et al., 2018) was used to perform these tests.

A second PERMANOVA was used to test the effects of habitat type on the community structures of Stilbaai, Goukamma, and Tsitsikamma. SIMPER tests were similarly used to identify the species which played the largest roles in the dissimilarity among the subset of study areas' habitat types. The adonis, vegdist, and simper functions (*vegan v2.4-2*) (Okansen et al., 2018) were used with the same non-default parameters as specified in the first PERMANOVA and SIMPER tests.

CAP ordination

Multivariate gradient analysis was used to create a visual representation of each of the 466 deployment sites in relation to one another based on each deployment site's study area, depth zone, and protection status. The Morisita-Horn dissimilarity index was selected to account for differences in the study areas' data set sizes (Chao et al., 2006).

The capscale function (distance = "horn", metaMDS = TRUE; *vegan v2.4-2*) (Okansen et al., 2018) was used to standardise the data and create a CAP ordination plot. The ordispider function (*vegan v2.4-2*) (Okansen et al., 2018) was used to enhance the interpretability of the ordination plot by grouping the sites by their respective study areas (Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma). The R ordiselect function (*goeveg v0.4.2*) (Friedmann & Schellenberg, 2018) was used to refine the species selection based on frequency and relative abundance values from the combined MPA data frame and overlay the ten most abundant species encountered throughout the four surveys onto the ordination plot based on their points of highest association.

CAP ordination, the Morisita-Horn dissimilarity index, and Wisconsin double standardisation are described in more detail in Chapter 2.

3.2.2 Network analysis of the MPAs' ichthyofaunal communities

The MPAs' ichthyofaunal communities were tested to determine whether they are complementary or offer redundancy of protection. Multi-level pattern analyses determine the strength and statistical significance of the relationship between species' relative abundances and physical and environmental variables (De Cáceres & Legendre, 2009; Hansen et al., 2016). They were used to determine which species associated with the following independent variables: study area, habitat type, and depth zone.

The multipatt function (*indicspecies v1.7.6*) (De Cáceres & Legendre, 2009) was used to create combinations of species and predictor variable clusters and determine the combinations with the highest association before testing them for significance. The multipatt function uses the indicator value index, as defined in De Cáceres & Legendre (2009), to determine the strength of species associations in individual site groups and in combinations of site groups by testing whether the null hypothesis that no association exists is true or not. The function compares an observed presence-absence test statistic with a randomly permuted distribution of the data (standardised to 999 permutations). The P-value produced by the multipatt function is the proportion of permutations that yielded equivalent or higher/lower association values than the observed data (De Cáceres & Legendre, 2009).

Complementarity and redundancy were determined by comparing the number of species that were represented in one or more of the four the MPAs. The more MPAs a species was represented in, the higher its redundancy of protection along the south coast. Complementarity was determined by the number of species recordings unique to each MPA.

3.4 Results

3.4.1 Comparison of the study areas' sampling distributions

The Goukamma survey had more than double the number of BRUV deployments than the other areas' surveys combined. The Betty's Bay survey had the next highest number of deployments, followed by the Tsitsikamma and Stilbaai surveys (Table 12).

The Stilbaai and Tsitsikamma surveys had similar habitat type ratios, both of which were biased toward reef sites. The Betty's Bay survey had more kelp forest sites than sand sites but was still predominantly biased towards reef sites. The Goukamma survey had the most balanced ratio been reef and sand sites (Figure 19).

The Tsitsikamma survey was biased towards shallow sites. The other three areas had relatively more even deployment ratios between the depth zones (Figure 20). The average depths of BRUV deployment sites in Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma were 21.5 m, 22 m, 22.7 m, and 19.5 m respectively. The Betty's Bay average was deduced from Roberson et al. (2015). The overall average depth of BRUV deployment sites among the four areas was 21.4 m.

The Betty's Bay and Goukamma surveys had relatively even sampling ratios between exploited and protected sites. No exploited sites were surveyed in the Stilbaai and Tsitsikamma surveys.

Table 12: Summary of BRUV deployments in Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma.

MPA	No. of successful BRUV deployments	Total no. of species	No. of unique species	No. of threatened species (IUCN)	Average no. of fish per deployment
Betty's Bay	58	42	6	7	38.5
Stilbaai	29	38	1	7	39.3
Goukamma	328	74	9	15	32.1
Tsitsikamma	51	69	2	14	53
Total	**466**	**88**	**18**	**17**	**40.7**

Each site represents an individual BRUV deployment in Figures 19 and 20.

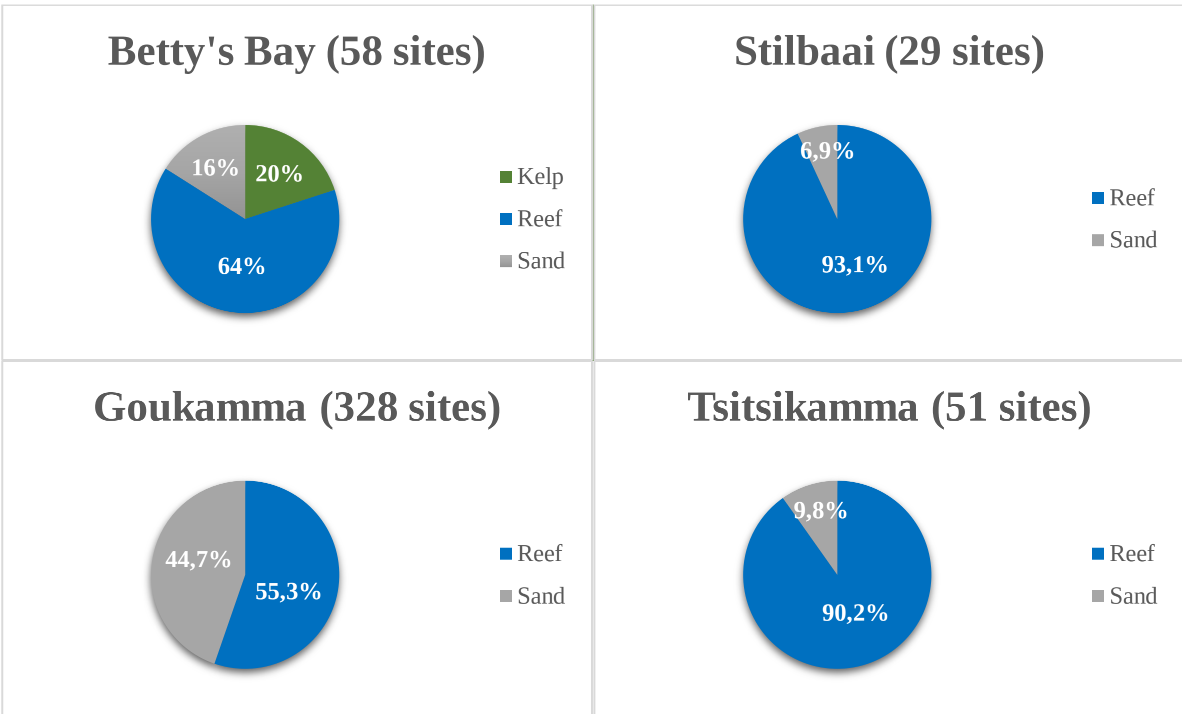

Figure 19: Habitat type ratios from each MPA survey.

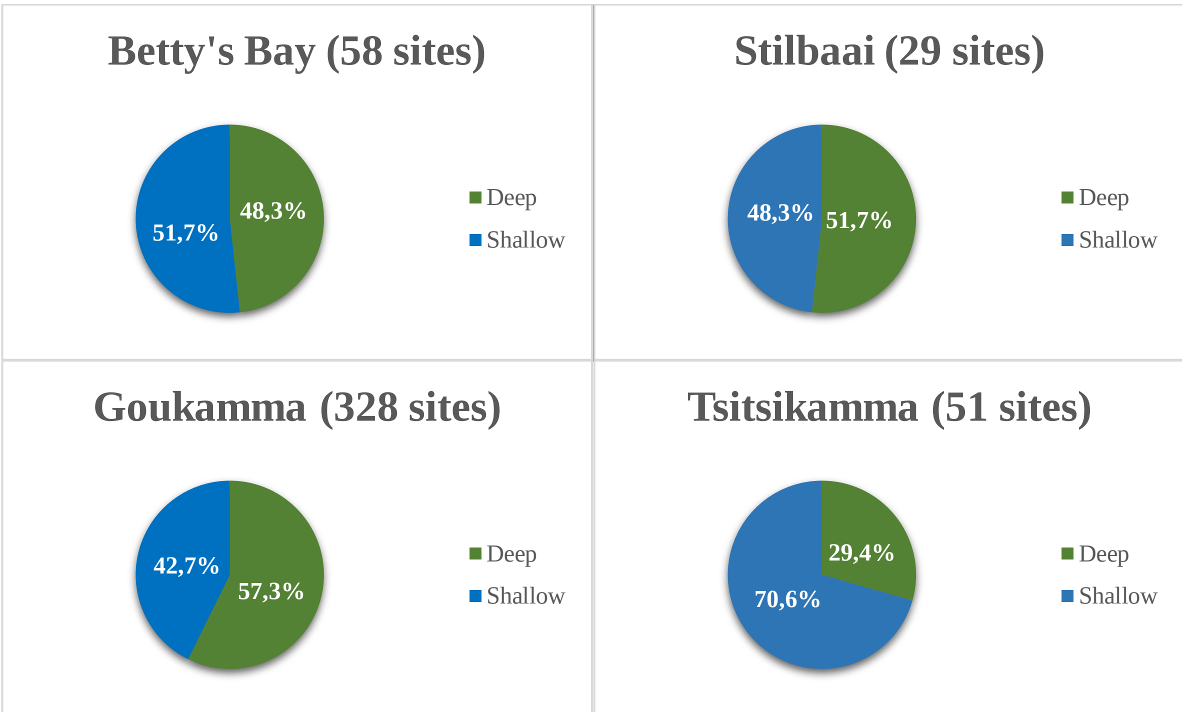

Figure 20: Depth zone ratios from each MPA survey (Shallow: 5-20 m and Deep: 20-42 m).

3.4.2 Distribution of species among the study areas

Twelve species were recorded in the Betty's Bay, Stilbaai, and/or Tsitsikamma surveys that were not present in Goukamma (Table 13). Five of these species were recorded in more than one of the other study areas i.e. *Argyrozona argyrozona*, *Haploblepharus pictus*, *Pachymetopon blochii*, *Rhabdosargus globiceps*, and *Sparodon durbanensis*. Four of these species are sparids and one is a scyliorhinid. The remaining eight species were only recorded in a single study area.

The Goukamma survey had the highest number of recorded species, followed by the Tsitsikamma, Betty's Bay, and Stilbaai surveys. Betty's Bay had 21 species in common with Stilbaai, 32 with Goukamma, and 34 with Tsitsikamma. Stilbaai had 35 species in common with Goukamma and 36 in common with Tsitsikamma. Goukamma had 62 species in common with Tsitsikamma (Table 14).

The six species records unique to the Betty's Bay survey were *Alopias vulpinus*, *Argyrosomus inodorus*, *Caffrogobius nudiceps*, *Chelidonichthys capensis*, *Congiopodus torvus*, and *Raja clavata*. *A. vulpinus* and *R. clavata* are marked as near threatened or worse on the IUCN Red List (Goldman et al., 2009; Ellis, 2016).
The single species record unique to the Stilbaai survey was *Epinephelus andersoni*, which is marked as near threatened on the IUCN Red List (Fennessy, 2018).

The nine species records unique to the Goukamma survey were *Callorhinchus capensis*, *Carcharodon carcharias*, *Cremnochorites capensis*, *Lagocephalus sceleratus*, *Mustelus palumbes*, *Narke capensis*, *Pomadasys striatus*, *Sphyrna zygaena*, and *Torpedo fuscomaculata*. *C. carcharias* and *S. zygaena* are marked as vulnerable on the IUCN Red List (Casper et al., 2009; Fergusson et al., 2009).

The two species records unique to the Tsitsikamma survey were *Etrumeus whiteheadi* and *Porcostoma dentata*, neither of which are marked for concern on the IUCN Red List.

Table 13: Species distribution among Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma.

Species	Presence/absence in each study area			
	Betty's Bay	Stilbaai	Goukamma	Tsitsikamma
Acanthistius sebastoides			X	X
Acroteriobatus annulatus			X	X
Alopias vulpinus	X			
Amblyrhynchotes honckenii		X	X	X
Argyrosomus inodorus	X			
Argyrosomus japonicus			X	X
Argyrozona argyrozona	X			X
Atractoscion aequidens	X		X	X
Boopsoidea inornata	X	X	X	X
Caffrogobius nudiceps	X			
Callorhinchus capensis			X	
Carcharhinus brachyurus		X	X	X
Carcharhinus obscurus			X	X
Carcharias taurus		X	X	X
Carcharodon carcharias			X	
Chaetodon marleyi		X	X	X
Cheilodactylus fasciatus	X	X	X	X
Cheilodactylus pixi	X		X	X
Cheimerius nufar		X	X	X
Chelidonichthys capensis	X			
Chelidonichthys kumu			X	X
Chirodactylus brachydactylus	X	X	X	X
Chirodactylus grandis	X		X	X
Chrysoblephus cristiceps		X	X	X
Chrysoblephus gibbiceps	X	X	X	X
Chrysoblephus laticeps	X	X	X	X
Clinus superciliosus	X		X	
Congiopodus torvus	X			
Cremnochorites capensis			X	
Cymatoceps nasutus		X	X	X
Bathytoshia brevicaudata	X	X	X	X
Dasyatis chrysonota		X	X	X
Dichistius capensis	X		X	
Diplodus capensis	X	X	X	X
Diplodus hottentotus	X	X	X	X
Epinephelus andersoni		X		
Epinephelus marginatus		X	X	X
Eptatretus hexatrema	X		X	X
Etrumeus whiteheadi				X
Galeichthys ater	X		X	X
Galeichthys feliceps	X	X	X	X
Galeorhinus galeus		X	X	X
Gymnocrotaphus curvidens	X	X	X	X
Gymnura natalensis	X		X	X
Halaelurus natalensis	X		X	X
Haploblepharus edwardsii	X	X	X	X
Haploblepharus fuscus			X	X
Haploblepharus pictus	X	X		X
Lagocephalus sceleratus			X	
Lichia amia			X	X
Lithognathus mormyrus			X	X

Table 13 (continued): Species distribution among Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma.

Species	Presence/absence in each study area			
	Betty's Bay	Stilbaai	Goukamma	Tsitsikamma
Mustelus mustelus	X	X	X	X
Mustelus palumbes			X	
Myliobatis aquila		X	X	X
Narke capensis			X	
Notorynchus cepedianus	X		X	X
Oplegnathus conwayi		X	X	X
Pachymetopon aeneum	X	X	X	X
Pachymetopon blochii	X			X
Pachymetopon grande	X	X	X	X
Pagellus natalensis			X	X
Parascorpis typus	X		X	X
Petrus rupestris	X	X	X	X
Polysteganus undulosus			X	X
Pomadasys olivaceus			X	X
Pomadasys striatus			X	
Pomatomus saltatrix			X	X
Porcostoma dentata				X
Poroderma africanum	X	X	X	X
Poroderma pantherinum	X	X	X	X
Pterogymnus laniarius	X	X	X	X
Raja clavata	X			
Raja straeleni			X	X
Rhabdosargus globiceps	X			X
Rhabdosargus holubi		X	X	X
Rostroraja alba			X	X
Sarpa salpa		X	X	X
Scyliorhinus capensis			X	X
Seriola lalandi			X	X
Serranus cabrilla			X	X
Sparodon durbanensis		X		X
Sphyrna zygaena			X	
Spondyliosoma emarginatum	X	X	X	X
Squalus megalops		X	X	
Torpedo fuscomaculata			X	
Trachurus trachurus	X		X	X
Triakis megalopterus	X	X	X	X
Umbrina robinsoni			X	X

Table 14: Triangular matrix of the number of species in common between each of the four study areas. Upper diagonal shows species richness at each study area.

	No. of species in common			
Study area	Betty's Bay	Stilbaai	Goukamma	Tsitsikamma
Betty's Bay	**42**			
Stilbaai	21	**38**		
Goukamma	32	35	**74**	
Tsitsikamma	34	36	62	**69**

3.4.3 Comparison of community structures

Study area was identified as a significant determinant of community structure composition along the south coast (PERMANOVA: $F = 27.1$, $P = 1.00 \times 10^{-3}$) (Table 15). SIMPER tests identified eight species that collectively contributed to over 50% of the dissimilarity in community structure composition among each of the four study areas: *Boopsoidea inornata*, *Chrysoblephus laticeps*, *Pachymetopon aeneum*, *Pachymetopon blochii*, *Pterogymnus laniarius*, *Spondyliosoma emarginatum*, *Sarpa salpa*, and *Trachurus trachurus*. *S. emarginatum* was the primary determinant of dissimilarity between each pair of study areas except Betty's Bay and Goukamma, where *T. trachurus* played a larger role in the areas' dissimilarity (Table 16).

Depth zone and protection status were also identified as significant in determining community structure composition along the south coast (PERMANOVA: $F = 17.4$, $P = 1.00 \times 10^{-3}$, and $F = 23.1$, $P = 1.00 \times 10^{-3}$, respectively) (Table 15). SIMPER tests identified six species that collectively contributed to over 50% of the dissimilarity in community structure composition between depth zones and protection statuses. *B. inornata*, *C. laticeps*, *T. trachurus*, *Poroderma africanum*, and *S. emarginatum* significantly affected community structure composition between shallow and deep zones along the south coast (Table 17). *P. laniarius* was substituted for *P. africanum* as a primary determinant of dissimilarity between exploited and protected zones along the south coast (Table 18). *S. emarginatum* played the largest role in determining dissimilarity between the depth zones and protection statuses.

Habitat type was identified as a significant determinant of community structure composition along the south coast when excluding the Betty's Bay survey sites from the MPA data frame (PERMANOVA: $F = 91.8$, $P = 1.00 \times 10^{-3}$) (Table 19). SIMPER tests identified four species that collectively contributed to over 50% of the dissimilarity in community structure composition between reef and sand sites: *B. inornata*, *C. laticeps*, *P. africanum*, and *S. emarginatum*. *S. emarginatum* played the largest role in determining dissimilarity in community structure composition between reef and sand sites along the south coast (Table 20).

The Goukamma and Tsitsikamma community structure clusters overlapped almost entirely on the CAP ordination plot, indicating that they had the two most similar community structures. They were the most diverse study areas. The Stilbaai cluster had a higher degree of overlap with the Goukamma and Tsitsikamma clusters than the Betty's Bay cluster, indicating a more similar community structure to the two larger study areas than its westward neighbour. Betty's Bay had the least similar community structure to the other three study areas (Figure 21).

Table 15: PERMANOVA test of the MPAs' species distribution data to determine whether study area, depth zone, and protection status significantly affected community structure compositions in the Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma surveys.

	Degrees of freedom	**Sum of squares**	**Mean of squares**	**F-value**	**Probability (>F)**	**Significance level**
Study area (SA)	3	18.8	6.3	27.1	1.0×10^{-3}	***
Depth zone (DZ)	1	4.0	4.0	17.4	1.0×10^{-3}	***
Protection status (PS)	1	5.3	5.3	23.1	1.0×10^{-3}	***
Two-way comparisons						
SA:DZ	3	3.2	1.1	4.7	1.0×10^{-3}	***
SA:PS	1	1.9	1.9	8.1	1.0×10^{-3}	***
DZ:PS	1	0.9	0.9	3.8	5.0×10^{-3}	**
Three-way comparison						
SA:DZ:PS	1	0.9	0.9	4.0	1.0×10^{-3}	***
Residuals	453	104.7	0.2			
Total	464	139.8				
Significance key:	"***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1	

Table 16: SIMPER test results for the study area variable.

Species	Average relative abundance in area A	Average relative abundance in area B	% of community composition	Cumulative sum
	Betty's Bay	**Stilbaai**		
S. emarginatum	0.8	12.6	19.34	0.1934
T. trachurus	15.7	0.0	17.24	0.3658
P. laniarius	5.4	0.8	7.27	0.4385
C. laticeps	1.1	5.1	7.11	0.5096
	Betty's Bay	**Goukamma**		
T. trachurus	15.7	0.4	20.02	0.2002
S. emarginatum	0.9	8.8	12.02	0.3204
P. laniarius	5.4	0.5	9.11	0.4115
P. blochii	3.9	0.0	7.08	0.4823
B. inornata	0.4	3.9	5.94	0.5417
	Betty's Bay	**Tsitsikamma**		
S. emarginatum	0.9	18.6	20.36	0.2036
T. trachurus	15.7	1.3	17.13	0.3749
B. inornata	0.4	7.4	7.91	0.4540
P. laniarius	5.4	0.5	7.28	0.5268
	Stilbaai	**Goukamma**		
S. emarginatum	12.62	8.8	28.36	0.2836
C. laticeps	5.1	3.2	9.19	0.3755
B. inornata	2.1	3.9	8.05	0.4560
S. salpa	4.5	0.4	6.34	0.5194
	Stilbaai	**Tsitsikamma**		
S. emarginatum	12.6	18.6	28.32	0.2832
B. inornata	2.1	7.4	10.22	0.3854
S. salpa	4.5	2.9	8.22	0.4676
C. laticeps	5.1	5.0	7.05	0.5381
	Goukamma	**Tsitsikamma**		
S. emarginatum	8.8	18.6	28.80	0.2880
B. inornata	3.9	7.4	12.04	0.4084
C. laticeps	3.2	5.0	8.14	0.4897
P. aeneum	1.5	2.5	4.58	0.5355

Table 17: SIMPER test results for the depth zone variable.

Species	Average relative abundance in shallow zone	Average relative abundance in deep zones	% of community composition	Cumulative sum
S. emarginatum	12.3	6.3	22.24	0.2224
B. inornata	5.4	2.3	9.98	0.3222
C. laticeps	3.3	3.2	7.44	0.3966
T. trachurus	2.2	2.6	6.31	0.4597
P. africanum	1.7	1.9	4.57	0.5054

Table 18: SIMPER test results for the protection status variable.

Species	Average relative abundance in exploited zones	Average relative abundance in protected zones	% of community composition	Cumulative sum
S. emarginatum	11.4	7.7	22.29	0.2229
B. inornata	5.3	2.7	10.70	0.3299
C. laticeps	3.4	3.2	7.40	0.4039
T. trachurus	2.6	2.2	6.54	0.4693
P. laniarius	2.4	1.5	4.89	0.5182

Table 19: PERMANOVA test of the MPAs' species distribution data to determine whether habitat type significantly affected community structure compositions in the Stilbaai, Goukamma, and Tsitsikamma surveys. Study area and protection status interactions could not be permuted due to the Stilbaai and Tsitsikamma data having no samples from exploited zones.

	Degrees of freedom	Sum of squares	Mean of squares	F-value	Probability (>F)	Significance level
Study area (SA)	2	3.4	1.7	8.8	1.0×10^{-3}	***
Habitat type (HT)	1	17.7	17.7	91.8	1.0×10^{-3}	***
Depth zone (DZ)	1	4.2	4.2	21.9	1.0×10^{-3}	***
Protection status (PS)	1	2.5	2.5	12.8	1.0×10^{-3}	***
Two-way comparisons						
SA:HT	2	0.7	0.4	1.9	0.059	.
SA:DZ	2	0.9	0.4	2.3	0.014	*
HT:DZ	1	1.6	1.6	8.1	1.0×10^{-3}	***
HT:PS	1	1.6	1.6	8.1	1.0×10^{-3}	***
DZ:PS	1	0.9	0.9	4.6	2.0×10^{-3}	**
Three-way comparisons						
SA:HT:DZ	1	0.6	0.6	3.3	4.0×10^{-3}	**
HT:DZ:PS	1	0.3	0.3	1.5	0.157	
Residuals	392	75.5	0.2			
Total	406	109.7				
Significance key:	"***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1	

Table 20: SIMPER test results for the habitat type variable.

Species	Average relative abundance over reef sites	Average relative abundance over sand sites	% of community composition	Cumulative sum
S. emarginatum	14.1	3.9	24.86	0.2486
B. inornata	6.3	0.6	11.84	0.3670
C. laticeps	5.0	1.1	10.90	0.4760
P. africanum	2.5	0.7	5.46	0.5306

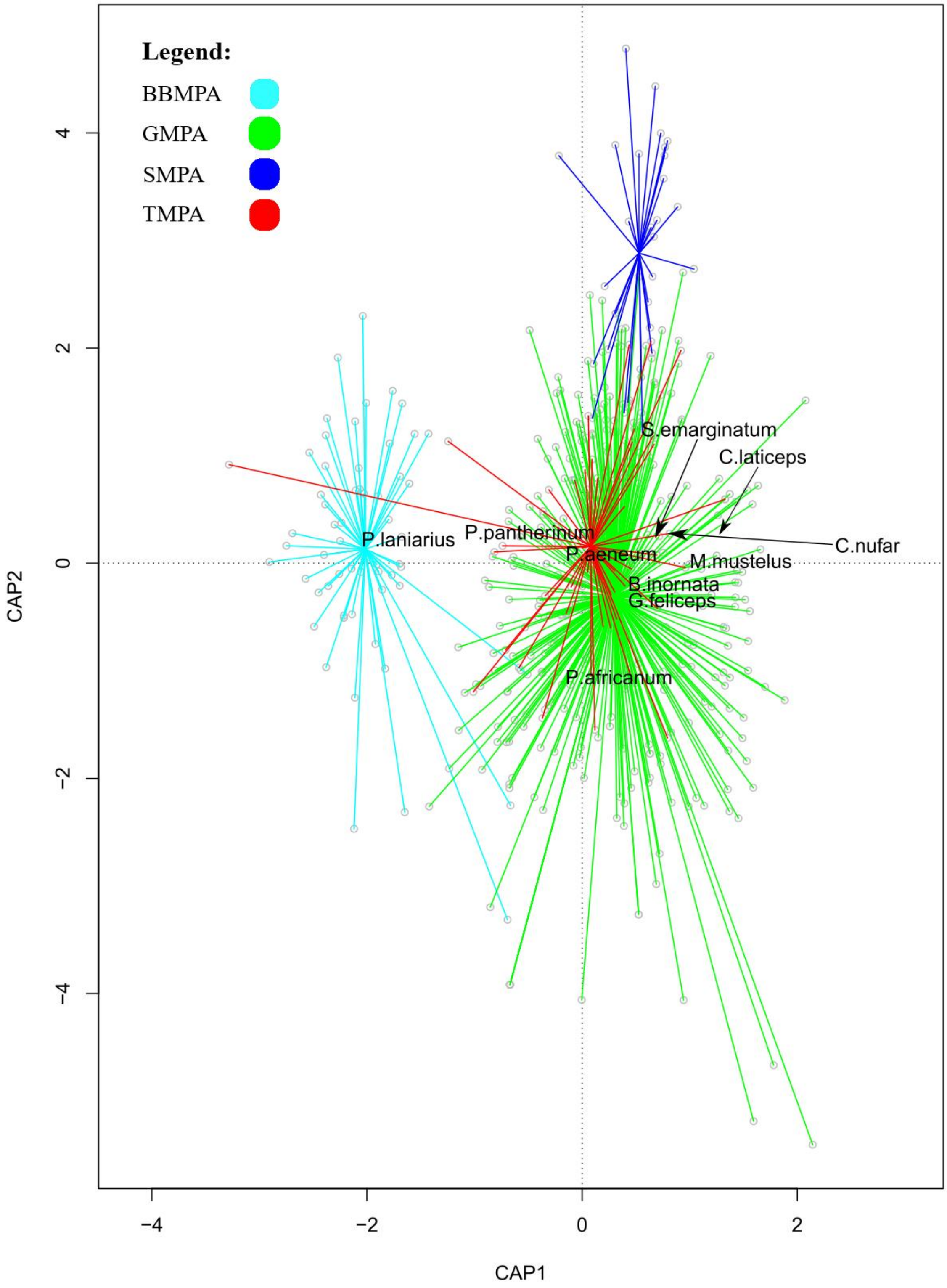

Figure 21: CAP ordination plot of the ichthyofaunal community structures in and around the BBMPA, GMPA, SMPA, and TMPA based on the species richness and abundances observed in 466 BRUV deployments. The ten species with the highest relative abundances are overlaid based on their points of highest association. *C. laticeps'*, *C. nufar's*, and *S. emarginatum's* positions were adjusted for clarity (see arrows for respective points of highest association).

3.4.4 Species' associations with study area, habitat type, and depth zone

Study area

There were 13 species significantly associated with Betty's Bay, two with Goukamma, ten with Stilbaai, and eight with Tsitsikamma. Eleven sparids associated with Tsitsikamma, nine with Stilbaai, and three with Betty's Bay and Goukamma respectively. Five chondrichthyans associated with Betty's Bay and Stilbaai respectively, four with Goukamma, and two with Tsitsikamma (Table 21). There was a single species significantly associated with each of area groups 1, 2, and 6, two with area groups 3 and 7, and three with area groups 4 and 5. There were no species significantly associated with all four MPAs (Table 22).

Habitat type

There were 25 species significantly associated with the reef and 14 with the sand. Almost 50% of the reef-associated species were sparids and 20% were chondrichthyans. The remaining reef-associated species included ariids, chaetodontids, cheilodactylids, and serranids. More than 75% of the sand-associated species were chondrichthyans. *P. natalensis* was the only sparid that associated with the sand. The remaining sand-associated species included ariids, tetradontids, and triglids (Table 23).

Depth zone

There were 27 species that were significantly associated with the shallow zone and three with the deep zone. Almost 50% of the shallow-associated species were sparids and over 20% were chondrichthyans. The remaining shallow-associated species included chaetodontids, cheilodactylids, clinids, myxinids, oplegnathids, and tetradontids. All of the deep-associated species were sparids (Table 24).

Associations grouped by family

The two ariids associated with different habitat niches. *G. ater* was associated with rocky reefs around Betty's Bay whereas *G. feliceps* was associated with sandy substrata in protected zones around Goukamma, Stilbaai, and Tsitsikamma.

The three carangids did not share any associations. *S. lalandi* was associated sandy substrata, *T. trachurus* with protected zones, and *T. trachurus* with Betty's Bay.

Cheilodactylids were associated with shallow rocky reefs around Betty's Bay and Tsitsikamma. *C. brachydactylus* was associated with shallow rocky reefs around Tsitsikamma, *C. fasciatus* with shallow rocky reefs around Betty's Bay and Tsitsikamma, *C. grandis* with Betty's Bay, and *C. pixi* with rocky reefs around Tsitsikamma.

Chondrichthyans were associated with shallow sandy substrata in protected zones around Betty's Bay, Goukamma, and Stilbaai. Carcharhinids were associated with protected zones around Stilbaai. Scyliorhinids were associated with shallow rocky reefs in exploited zones around Betty's Bay, Goukamma, and Stilbaai. Skates and rays, in this case dasyatids, myliobatids, rajids, and rhinobatids, were associated with shallow sandy substrata in protected zones around Goukamma. Triakids were associated with shallow sandy substrata around Goukamma, Stilbaai, and Tsitsikamma.

A. annulatus and *H. natalensis* were associated with sandy substrata in protected zones. *Callorhinchus capensis*, *R. alba*, *R. straeleni*, *S. zygaena*, and *S. megalops* were associated with sandy substrata. *C. brachyurus* was associated with protected zones around Stilbaai. *C. obscurus* was associated with protected zones. *C. taurus* was associated with shallow waters. *D. chrysonota* was associated with shallow sandy substrata. *G. galeus* and *T. megalopterus* were associated with shallow waters around Stilbaai. *H. edwardsii* was associated with rocky reefs around Betty's Bay. *H. fuscus* was associated with rocky reefs around Goukamma. *H. pictus* was associated with shallow rocky reefs around Betty's Bay. *M. mustelus* was associated with shallow sandy substrata around Goukamma, Stilbaai, and Tsitsikamma. *M. aquila* was associated with shallow waters around Goukamma. *N. cepedianus* was associated with Betty's Bay. *P. africanum* was associated with rocky reefs in exploited zones around Betty's Bay, Goukamma, and Stilbaai. *P. pantherinum* was associated with rocky reefs in exploited zones around Betty's Bay and Stilbaai.

Serranids were associated with rocky reefs in exploited zones around Goukamma, Stilbaai, and Tsitsikamma. *A. sebastoides* was associated with rocky reefs around Goukamma and Tsitsikamma, *E. marginatus* with rocky reefs in exploited zones around Goukamma and Stilbaai, and *S. cabrilla* with rocky reefs.

Sparids were associated with shallow rocky reefs in exploited zones around Stilbaai and Tsitsikamma, however, it must be noted that no exploited waters were sampled in either of these areas. Despite a lower association to Betty's Bay and Goukamma, the populations of sparids in their exploited zones were significant enough to skew the overall association of the group. Sparids were the most diverse group of fish sampled and occupied all depth zone, habitat, study area, and protection zone niches.

A. argyrozona and *P. undulosus* were associated with deep waters. *B. inornata* was associated with shallow rocky reefs in exploited zones around Goukamma and Tsitsikamma. *C. nufar* was associated with exploited zones around Goukamma and Stilbaai. *C. cristiceps* and *S. emarginatum* were associated with shallow rocky reefs in exploited zones around Tsitsikamma. *C. gibbiceps* was associated with rocky reefs in exploited zones around Stilbaai. *C. laticeps* was associated with rocky reefs in exploited zones around Stilbaai and Tsitsikamma. *C. nasutus* was associated with shallow waters around Stilbaai. *Diplodus capensis* and *R. holubi* were associated with shallow rocky reefs in protected zones around Tsitsikamma. *D. hottentotus* and *P. rupestris* were associated with shallow rocky reefs in exploited zones around Stilbaai. *G. curvidens* and *S. salpa* were associated with shallow rocky reefs around Stilbaai and Tsitsikamma. *L. mormyrus* was associated with shallow waters. *P. aeneum* was associated with rocky reefs in exploited zones. *P. blochii* was associated with Betty's Bay. *P. natalensis* was associated with shallow sandy substrata in protected zones around Goukamma and Tsitsikamma. *P. laniarius* was associated with deep waters around Betty's Bay. *R. globiceps* was associated with shallow waters around Tsitsikamma.

The following group is made up of families represented by a single species in the multi-level pattern analyses and includes a species from the clinids, the chaetodontids, the dichistiids, the haemulids, the myxinids, the oplegnathids, the tetradontids, and the triglids.

A. honckenii was associated with shallow sandy substrata in protected zones around Stilbaai. *C. supercilious* and *E. hexatrema* were associated with shallow waters around Betty's Bay. *C. marleyi* and *O. conwayi* were associated with shallow rocky reefs in exploited zones. *Chelidonichthys capensis* was associated with sandy substrata around Betty's Bay. *Dichistius capensis* was associated with Betty's Bay. *P. olivaceus* was associated with protected zones.

Figure 22: Redundancy of protection of species among the four MPAs.

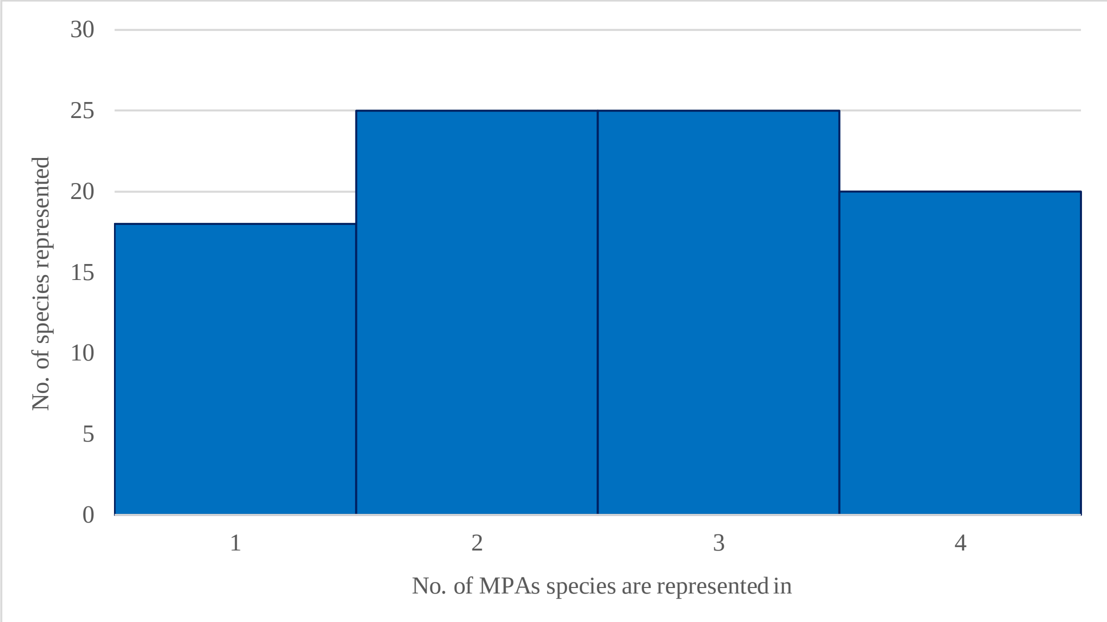

Table 21: Species significantly associated with either Betty's Bay, Stilbaai, Goukamma, or Tsitsikamma.

Species	Family	Test statistic	P-value	Significance
	Betty's Bay			
Galeichthys ater	Ariidae	0.254	0.005	**
Trachurus trachurus	Carangidae	0.385	0.005	**
Chirodactylus grandis	Cheilodactylidae	0.24	0.005	**
Clinus superciliosus	Clinidae	0.333	0.005	**
Dichistius capensis	Dichistiidae	0.173	0.025	*
Notorynchus cepedianus	Hexanchidae	0.595	0.005	**
Eptatretus hexatrema	Myxinidae	0.39	0.005	**
Haploblepharus edwardsii	Scyliorhinidae	0.436	0.005	**
Haploblepharus pictus	Scyliorhinidae	0.582	0.005	**
Argyrozona argyrozona	Sparidae	0.28	0.005	**
Pachymetopon blochii	Sparidae	0.693	0.005	**
Pterogymnus laniarius	Sparidae	0.551	0.005	**
Chelidonichthys capensis	Triglidae	0.213	0.015	*
	Stilbaai			
Carcharhinus brachyurus	Carcharhinidae	0.254	0.005	**
Epinephelus andersoni	Epinephelidae	0.255	0.005	**
Chrysoblephus gibbiceps	Sparidae	0.154	0.015	*
Cymatoceps nasutus	Sparidae	0.293	0.005	**
Diplodus hottentotus	Sparidae	0.162	0.015	*
Petrus rupestris	Sparidae	0.272	0.005	**
Sparodon durbanensis	Sparidae	0.294	0.005	**
Amblyrhynchotes honckenii	Tetraodontidae	0.141	0.005	**
Galeorhinus galeus	Triakidae	0.289	0.005	**
Triakis megalopterus	Triakidae	0.129	0.045	*

Table 21 (continued): Species significantly associated with either Betty's Bay, Stilbaai, Goukamma, or Tsitsikamma.

Species	Family	Test statistic	P-value	Significance
	Goukamma			
Myliobatis aquila	Myliobatidae	0.17	0.01	**
Haploblepharus fuscus	Scyliorhinidae	0.171	0.015	*
	Tsitsikamma			
Cheilodactylus pixi	Cheilodactylidae	0.131	0.01	**
Chirodactylus brachydactylus	Cheilodactylidae	0.124	0.04	*
Chrysoblephus cristiceps	Sparidae	0.237	0.005	**
Diplodus capensis	Sparidae	0.232	0.005	**
Porcostoma dentata	Sparidae	0.178	0.02	*
Rhabdosargus globiceps	Sparidae	0.185	0.01	**
Rhabdosargus holubi	Sparidae	0.342	0.005	**
Spondyliosoma emarginatum	Sparidae	0.214	0.005	**
Significance key: "***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1

Table 22: Species significantly associated with two or more of the study areas.

Species	Family	Test statistic	P-value	Significance
	Betty's Bay and Stilbaai (Study area group 1)			
Poroderma pantherinum	Scyliorhinidae	0.213	5.0×10^{-3}	**
	Betty's Bay and Tsitsikamma (Study area group 2)			
Cheilodactylus fasciatus	Cheilodactylidae	0.272	5.0×10^{-3}	**
	Stilbaai and Goukamma (Study area group 3)			
Epinephelus marginatus	Serranidae	0.118	0.030	*
Cheimerius nufar	Sparidae	0.201	0.010	**
	Goukamma and Tsitsikamma (Study area group 4)			
Acanthistius sebastoides	Serranidae	0.185	5.0×10^{-3}	**
Boopsoidea inornata	Sparidae	0.218	5.0×10^{-3}	**
Pagellus natalensis	Sparidae	0.127	0.040	*
	Stilbaai and Tsitsikamma (Study area group 5)			
Chrysoblephus laticeps	Sparidae	0.282	5.0×10^{-3}	**
Gymnocrotaphus curvidens	Sparidae	0.227	5.0×10^{-3}	**
Sarpa salpa	Sparidae	0.202	5.0×10^{-3}	**
	Betty's Bay, Goukamma, and Tsitsikamma (Study area group 6)			
Poroderma africanum	Scyliorhinidae	0.162	5.0×10^{-3}	**
	Stilbaai, Goukamma, and Tsitsikamma (Study area group 7)			
Galeichthys feliceps	Ariidae	0.136	0.040	*
Mustelus mustelus	Triakidae	0.236	5.0×10^{-3}	**
Significance key: "***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1

Table 23: Species significantly associated with shallow and deep zones along the south coast.

Species	Family	Test statistic	P-value	Significance
		Shallow zone		
Chaetodon marleyi	Chaetodontidae	0.137	$5.0x10^{-3}$	**
Cheilodactylus fasciatus	Cheilodactylidae	0.121	0.015	*
Chirodactylus brachydactylus	Cheilodactylidae	0.16	$5.0x10^{-3}$	**
Clinus superciliosus	Clinidae	0.13	$5.0x10^{-3}$	**
Dasyatis chrysonota	Dasyatidae	0.131	0.010	**
Myliobatis aquila	Myliobatidae	0.098	0.050	*
Eptatretus hexatrema	Myxinidae	0.114	0.030	*
Carcharias taurus	Odontaspididae	0.12	0.025	*
Oplegnathus conwayi	Oplegnathidae	0.135	0.005	**
Haploblepharus pictus	Scyliorhinidae	0.111	0.025	*
Boopsoidea inornata	Sparidae	0.254	$5.0x10^{-3}$	**
Chrysoblephus cristiceps	Sparidae	0.103	0.045	*
Cymatoceps nasutus	Sparidae	0.115	$5.0x10^{-3}$	**
Diplodus capensis	Sparidae	0.225	$5.0x10^{-3}$	**
Diplodus hottentotus	Sparidae	0.155	0.010	**
Gymnocrotaphus curvidens	Sparidae	0.107	0.030	*
Lithognathus mormyrus	Sparidae	0.132	$5.0x10^{-3}$	**
Pagellus natalensis	Sparidae	0.100	0.045	*
Petrus rupestris	Sparidae	0.144	0.050	**
Rhabdosargus globiceps	Sparidae	0.075	0.020	*
Rhabdosargus holubi	Sparidae	0.174	$5.0x10^{-3}$	**
Sarpa salpa	Sparidae	0.14	$5.0x10^{-3}$	**
Spondyliosoma emarginatum	Sparidae	0.217	$5.0x10^{-3}$	**
Amblyrhynchotes honckenii	Tetraodontidae	0.292	$5.0x10^{-3}$	**
Galeorhinus galeus	Triakidae	0.180	$5.0x10^{-3}$	**
Mustelus mustelus	Triakidae	0.142	0.010	**
Triakis megalopterus	Triakidae	0.109	0.015	*
		Deep zone		
Argyrozona argyrozona	Sparidae	0.088	0.010	**
Polysteganus undulosus	Sparidae	0.108	0.020	*
Pterogymnus laniarius	Sparidae	0.258	$5.0x10^{-3}$	**
Significance key: "***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1

Table 24: Species significantly associated with reef and sand sites in Stilbaai, Goukamma, and Tsitsikamma.

Species	Family	Test statistic	P-value	Significance
		Reef		
Galeichthys ater	Ariidae	0.201	$5.0x10^{-3}$	**
Chaetodon marleyi	Chaetodontidae	0.146	0.010	**
Chirodactylus brachydactylus	Cheilodactylidae	0.401	$5.0x10^{-3}$	**
Cheilodactylus fasciatus	Cheilodactylidae	0.221	$5.0x10^{-3}$	**
Cheilodactylus pixi	Cheilodactylidae	0.26	$5.0x10^{-3}$	**
Oplegnathus conwayi	Oplegnathidae	0.194	$5.0x10^{-3}$	**
Haploblepharus edwardsii	Scyliorhinidae	0.148	0.010	**
Haploblepharus fuscus	Scyliorhinidae	0.125	0.020	*
Poroderma africanum	Scyliorhinidae	0.425	$5.0x10^{-3}$	**
Poroderma pantherinum	Scyliorhinidae	0.326	$5.0x10^{-3}$	**
Acanthistius sebastoides	Serranidae	0.308	$5.0x10^{-3}$	**

Table 24 (continued): Species significantly associated with reef and sand sites in Stilbaai, Goukamma, and Tsitsikamma.

Species	Family	Test statistic	P-value	Significance
		Reef (continued)		
Epinephelus marginatus	Serranidae	0.2	$5.0x10^{-3}$	**
Serranus cabrilla	Serranidae	0.127	0.015	*
Boopsoidea inornata	Sparidae	0.433	$5.0x10^{-3}$	**
Chrysoblephus cristiceps	Sparidae	0.306	$5.0x10^{-3}$	**
Chrysoblephus gibbiceps	Sparidae	0.24	$5.0x10^{-3}$	**
Chrysoblephus laticeps	Sparidae	0.633	$5.0x10^{-3}$	**
Diplodus capensis	Sparidae	0.242	$5.0x10^{-3}$	**
Diplodus hottentotus	Sparidae	0.334	$5.0x10^{-3}$	**
Gymnocrotaphus curvidens	Sparidae	0.246	$5.0x10^{-3}$	**
Pachymetopon aeneum	Sparidae	0.262	$5.0x10^{-3}$	**
Petrus rupestris	Sparidae	0.268	$5.0x10^{-3}$	**
Rhabdosargus holubi	Sparidae	0.106	0.030	*
Sarpa salpa	Sparidae	0.116	0.015	*
Spondyliosoma emarginatum	Sparidae	0.328	$5.0x10^{-3}$	**
		Sand		
Galeichthys feliceps	Ariidae	0.102	0.050	*
Callorhinchus capensis	Callorhinchidae	0.13	0.035	*
Seriola lalandi	Carangidae	0.093	0.050	*
Dasyatis chrysonota	Dasyatidae	0.133	0.010	**
Raja straeleni	Rajidae	0.13	0.045	*
Rostroraja alba	Rajidae	0.182	$5.0x10^{-3}$	**
Acroteriobatus annulatus	Rhinobatidae	0.211	$5.0x10^{-3}$	**
Halaelurus natalensis	Scyliorhinidae	0.327	$5.0x10^{-3}$	**
Pagellus natalensis	Sparidae	0.244	$5.0x10^{-3}$	**
Sphyrna zygaena	Sphyrnidae	0.214	$5.0x10^{-3}$	**
Squalus megalops	Squalidae	0.181	$5.0x10^{-3}$	**
Amblyrhynchotes honckenii	Tetraodontidae	0.275	$5.0x10^{-3}$	**
Mustelus mustelus	Triakidae	0.185	$5.0x10^{-3}$	**
Chelidonichthys kumu	Triglidae	0.13	0.015	*

Significance key:	"***" = 0.001	"**" = 0.01	"*" = 0.05	"." = 0.1	" " = 1

3.5 Discussion

3.5.1 Community structures and redundancy of protection among Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma

Sample size was not a predominant determinant of species richness along the south coast. The highest sampling effort among the study areas took place in Goukamma, where the highest species richness was recorded, however, species richness was not proportionate to sampling effort. There were 84% more BRUVs deployed in Goukamma than Tsitsikamma, but only 7% more species were recorded in Goukamma than the Tsitsikamma. Sampling effort was 12% higher in Betty's Bay than Tsitsikamma, but 39% less species were recorded in the Betty's Bay than the Tsitsikamma.

All four areas' average site depths ranged between 19.5-22.7 m. Depth zone played a significant role in determining species richness and abundance in each study area, but the similarity of the areas' depth sampling profiles likely means it had little affect on differences in community structure among the areas.

Protected areas play a positive role in fish size and abundance in Betty's Bay (Roberson et al., 2015), Goukamma (Götz, 2005), and Tsitsikamma (Buxton & Smale, 1989), the Goukamma BRUV survey identified that species richness and abundance were more significantly linked to habitat type than protection status. Sampling in Stilbaai and Tsitsikamma was exclusively conducted in protected zones and the relative abundance of sparids was higher than in Betty's Bay and Goukamma, where both exploited and protected zones were sampled.

Underrepresentation of reef in Goukamma's protected zones is the likely reason the MPA had lower numbers of sparids and other reef-associated species per BRUV deployment than Stilbaai and Tsitsikamma. A balancing of the GMPA's protected habitat type ratio to increase reef inclusivity has the potential to elevate the species richness and abundance of the area's protected zones above that of its exploited zones and would likely be more comparable with Stilbaai and Tsitsikamma. Betty's Bay was the only study area which was not dominated by reef-associated sparids. It exhibited a divergence in community structure from its eastward counterparts and was dominated by carangids, scyliorhinids, and a mix of reef- and sand-associated sparids (Binohlan & Luna, 2019b; Luna & Reyes, 2019).

T. trachurus significantly associated with Betty's Bay and schools of over 200 specimens were observed in and around the MPA. It is not a shallow-associated species but uses kelp forests as nursery areas to increase recruitment potential (Vandendriessche et al., 2007). The carangid predates on juvenile squid and benthic invertebrates (Smith-Vaniz et al., 2015), and is potentially drawn to the abundance of chokka squid (*Loligo reynaudii*) observed during the Betty's Bay survey (Roberson et al., 2015).

A. argyrozona, *P. blochii*, and *P. laniarius* were the only sparids significantly associated with Betty's Bay. Squid are one of the primary constituents of *A. argyrozona'* diet (Mann, et al., 2014g), and both *P. blochii* and *P. laniarius* feed on species associated with kelp forests (sea urchins and brittle stars respectively) (Graham, 2004; Mann et al., 2014g,h). The increased abundance of their respective dietary constituents as a result of the kelp forests is likely the reason that they are able to successfully co-exist with the schools of *T. trachurus* in the area.

Habitat type was the most significant determinant of community structure composition along the south coast. Betty's Bay had the most complex habitat structure of the four study areas and subsequently had the most unique community structure. Whilst protection status is the most important variable in MPA management (Mosquera et al., 2000), it is essential that protected areas are zoned such that they most effectively conserve an areas' predominant habitat types, so as to avoid scenarios as observed in Goukamma, where imbalanced zoning has lead to ineffective protection of key species.

All four study areas offer redundancy of protection for 20 species of fish, including 11 species of sparids and six species of chondrichthyans. Stilbaai, Goukamma, and Tsitsikamma were dominated by four sparid species: *B. inornata*, *C. laticeps*, *P. aeneum*, and *S. emarginatum.* Differences in their community structures was primarily due to significantly more *S. emarginatum* in Goukamma than in Stilbaai and Tsitsikamma, however, it was still a dominant species in both of these areas. Eighty percent of species were represented in more than one of the four MPAs, indicating a high level of redundancy of protection along the south coast.

Of the 88 species recorded among the four study areas, 18 were recorded in less than two MPAs. Goukamma had the highest number of unique species observations, followed by Betty's Bay, Tsitsikamma, and Stilbaai. Majority of Goukamma's unique species observations were chondrichthyans and offered the high complementarity for these species. Betty's Bay had the most unique community structure of the four areas and offered the highest complementarity for reef- and kelp-associated species.

Diversity did not proportionately correlate with MPA size, as the Tsitsikamma MPA is more than four times the size of the Goukamma MPA but had a lower species richness. Similarity in community structure was not linked to the study areas' geographic proximity to one another. Betty's Bay was least similar to the area closest to it and most similar to the area furthest away. Stilbaai was more similar to Tsitsikamma than Goukamma, which is situated in between them. Geographic proximity is not a good predictor of ichthyofaunal community structure, as it does not account for the effects of localised physical and environmental variables, however, the study area's geographic positions along the coast and their distance from the continental shelf break may play an important role in their relative abundances.

3.5.2 Subtropical subtraction along the south coast

South Africa's continental shelf extends further from the coastline as one moves from east to west along the south coast (Griffiths et al., 2010). A subsurface cold-water ridge exists along the shelf break of the Agulhas Bank, which is associated with increased copepod and phytoplankton concentrations (Hutchings et al., 2002). The cold-water ridge is the result of strong easterly winds during summer. Goukamma and Tsitsikamma are closer to the shelf break as they are further east than the other two study areas, and their capacity to support larger and more diverse community structures is likely supplemented by the surplus of available sustenance stemming from their proximity to the cold-water ridge. Their proximity to the 200 m contour also means that species that normally associate with deeper habitats might more commonly venture into the Goukamma and Tsitsikamma systems. Potential examples of this phenomenon are *Callorhinchus capensis* and *S. capensis*, both of which have depth ranges exceeding 300 m and were only recorded in Goukamma and Tsitsikamma (Pheeha & Dagit, 2006; Carpenter & Luna, 2019a). Whilst geographic proximity is not a significant predictor variable in determining community structure along the south coast, geographic position appears to be, which matches Turpie et al.'s (2000) findings on the effects of subtropical subtraction: species richness decreases along South Africa's south coast from east to west.

Species richness almost halved from the eastern extreme of the study area to the western extreme, however, Betty's Bay had a slightly higher species abundance than Stilbaai to its east.

This is likely due to Betty's Bay having a more diverse habitat structure than Stilbaai. The predominant kelp species making up Betty's Bay's forests is *Ecklonia maxima* (Roberson et al., 2015), which can reach lengths of up to 8 m. These forests extend the vertical potential of the benthos as nursery areas and refuges for organisms that would otherwise be constrained to the seafloor. *C. nudiceps* is an example of a species that associates with kelp forests that was only observed in Betty's Bay (Sa-a & Reyes, 2019).

The south coast's overall relative abundance gradient did not match the species richness trend, however, sparids (notably *C. cristiceps*, *C. gibbiceps*, and *C. laticeps*) and other endangered and important fishery species had higher relative abundances in Goukamma, Stilbaai, and Tsitsikamma than Betty's Bay. Demersal chondrichthyans such as the scyliorhinids were more associated with the west and species such as the triakids were more associated with the east. Benthic invertebrates and cephalopods make up a large portion of scyliorhinids diets (Carpenter & Capuli, 2019; Carpenter & Luna, 2019d), and the increased numbers of squid and juvenile rock lobster could account for their elevated abundance in the west.

The lowest overall average abundance per site was recorded in the middle of the south coast in Goukamma. This is potentially attributable to Goukamma having the most even habitat type ratio among the four surveys and having almost four times more sand sites surveyed than any of the other areas. Betty's Bay had a similar ratio of non-reef sites surveyed to Goukamma, but over a fifth of these sites were kelp forests and not sandy substrata. If Betty's Bay's kelp forests are considered closer to reef than sand (Graham, 2004), then the Betty's Bay survey's habit type ratio was much closer to the Stilbaai and Tsitsikamma surveys' ratios than the Goukamma survey's ratio. Stilbaai and Tsitsikamma had similar habitat type ratios but Tsitsikamma had a higher average abundance per deployment, which could be a result of increased species richness due to the Agulhas cold-water ridge.

Conclusion

Sparids dominated the shallow subtidal sections of the Goukamma MPA and surrounding waters and co-existed with a diverse range of chondrichthyans. Sharks were well represented in the NTZ, which is a sign of a functional and healthy ecosystem (Fulton et al., 2005). The presence of rocky reefs was the most significant factor in determining species composition and abundance. The current imbalance in the GMPA's habitat ratio was reflected by higher concentrations of sparids and other reef-associated fish in Goukamma's exploited zones. Extending the GMPA's seaward boundary to include the NNTZ could potentially positively impact both reef- and sand-associated communities by increasing the ratio of protected reef and creating a buffer between the predominantly sand-based NTZ and the GMPA's seaward boundary. The NNTZ is a more suitable option for protection than the EZ, as it will have less of an impact on local stakeholders making use of the area's western reefs and oyster beds.

A higher percentage of protected reef would also likely lead to increased positive spillover into exploited zones and increase the overall CPUE of Goukamma's recreational and commercial fishers, a phenomenon which has already been observed in the area's *C. laticeps* population (Götz, 2005). Sparids are one of the most overexploited components of South Africa's linefisheries and chondrichthyan populations are in a state of decline around the world (Griffiths, 2000; Baum et al., 2003; Robbins et al., 2006). The protection of the NNTZ might serve to further bolster these vulnerable species' populations along South Africa's south coast.

The BRUV survey of Goukamma produced a larger and more diverse data set than previous CAS and UVC survey and were especially effective at recording chondrichthyans, which were not well represented by the other two survey methods. BRUV and UVC surveys were both effective methods for measuring sparid diversity and abundance. The CAS consistently recorded the lowest number of fish per sampling effort but did record more species than UVC survey. BRUVs have the potential to become the predominant survey method for determining ichthyofaunal community structures and would be most effective if upgraded to stereo-BRUVs to allow for the approximation of specimen sizes.

Analysis of the combined MPA fish community data indicated that community structure differed among Betty's Bay, Stilbaai, Goukamma, and Tsitsikamma. Habitat type was identified as the primary determinant of community structure composition. Betty's Bay's divergence from the sparid-dominated community structures observed in Stilbaai, Goukamma, and Tsitsikamma was because of kelp forests in and around the MPA. The kelp forests provide a refuge and feeding niche for kelp-associated species that are potentially outcompeted by the reef-associated sparids in barren habitat and supported a more diverse representation of families than was observed in the other three study areas.

All four study areas offered redundancy of protection for several species of ariids, cheilodactylids, sparids, and chondrichthyans. Betty's Bay had the most unique community structure and offered the least redundancy of protection, whilst Goukamma and Tsitsikamma offered the highest. Goukamma had the most diverse representation of chondrichthyans but was still exhibited a similar sparid-dominance to Stilbaai and Tsitsikamma. Despite having the most unique community structure along the south coast, Betty's Bay's was less diverse than Goukamma and Tsitsikamma. This is due to Betty's Bay's position on the west-side of the south coast and Goukamma and Tsitsikamma's positions on the east-side, where their ichthyofaunal communities benefit from elevated concentrations of copepods and phytoplankton as a result of increased proximity to the Agulhas cold-water ridge.

Sparids and other important reef fishery species had higher relative abundances in the east. Chondrichthyans that predate on these species were more associated with the east and demersal chondrichthyans that predate on benthic invertebrates and cephalopods were more associated with the west. Species associations with physical and environmental variables are a result of the variables' potential to increase food availability and recruitment. The size and diversity of community structures along South Africa's south coast were observed to increase from west to east as a result of this. Review of the De Hoop and Bird's Island fish community data collected by Heyns-Veale et al. (2019) should be conducted to further examine the effects of subtropical subtraction along South Africa's south coast.

South Africa was ranked in the top 20% of countries around the world and third in Africa for its level of marine protection in 2018 (UNEP-WCMC & IUCN, 2020), and has likely increased in both rankings since the establishment of 21 new MPAs in 2019. The future and sustainability of the country's ichthyofaunal resources are currently in a comparatively good standing when compared to other countries around the world, which only further highlights the need for continued MPA-based monitoring and optimisation in South Africa.

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Appendices

Appendices 1 and 2 offer supplementary reference material that was too cumbersome to provide in the form of in-text citations. Appendix 1 is a list of the individual government gazettes for the 20 new MPAs declared under Operation Phakisa and their respective references. Appendix 2 is a list of MPAs and other areas around the world where BRUVS have been used to monitor ichthyofaunal populations.

Appendix 1

Table I: Operation Phakisa MPA gazettes.

Operation Phakisa MPAs and expansions	Gazette reference
Addo Elephant National Park	DEA SA, 2019c
Agulhas Bank Complex	DEA SA, 2019d
Agulhas Front	DEA SA, 2019e
Agulhas Muds	DEA SA, 2019f
Aliwal Shoal (expansion)	DEA SA, 2019g
Amathole Offshore (expansion)	DEA SA, 2019h
Benguela Muds	DEA SA, 2019i
Browns Bank Corals	DEA SA, 2019j
Cape Canyon	DEA SA, 2019k
Childs Bank	DEA SA, 2019l
iSimangaliso (expansion)	DEA SA, 2019m
Namaqua Fossil Forest	DEA SA, 2019n
Namaqua National Park	DEA SA, 2019o
Orange Shelf	DEA SA, 2019p
Port Elizabeth Corals	DEA SA, 2019q
Protea Banks	DEA SA, 2019r
Robben Island	DEA SA, 2019s
Southeast Atlantic Seamounts	DEA SA, 2019t
Southwest Indian Seamount	DEA SA, 2019u
uThukela	DEA SA, 2019v

Appendix 2

Table II: Examples of the use of BRUVS in MPAs and other areas of ecological interest around the world.

Country	Location	Reference
American Samoa (USA)	Taena Bank	Barord et al., 2014
Australia	Bennett's Beach	Harasti et al., 2017
	Commonwealth Marine Reserve Network	Hill et al., 2014
	Coral Bay	Santana-Garcon et al., 2014
	Glover's Reef Marine Reserve	Bond et al., 2012
	Great Barrier Reef	Cappo et al., 2004; Barord et al., 2014
	Hamelin Bay	Watson et al., 2005
	Houtman Abrolhos Islands	Watson et al., 2010; Dorman et al., 2012; Harvey et al., 2012
	Ningaloo Reef	Westera et al., 2003; Watson et al., 2010
	South Australian Marine Parks Program	Miller et al., 2017
Bahamas	Cape Eleuthera	Brooks et al., 2011
Borneo (Malaysia)	Kapalai and Mabul Islands; Tunku Abdul Rahman Park; Tun Sakaran Marine Park	Sherman et al., 2018
Brazil	Xingu River	Schmid et al., 2017
England	Plymouth Mudflats	Sheehan et al., 2010
Fiji	Beqa Passage – Viti Levu	Barord et al., 2014
	Vanua Levu Island MPAs	Goetze et al., 2011
France	Western Mediterranean	Stobart et al., 2007
Indonesia	Raja Ampat MPA Network	Beer, 2015
Malaysia	Tioman Island	Yoshida et al., 2010
New Caledonia (France)	South-west Lagoon	Langlois et al., 2006
New Zealand	Cape Rodney-Okakari Point MPA; Hahei MPA; Leigh MPA	Willis et al., 2000
	Mimiwhangata Marine Park	Denny & Babcock, 2004
	Northern coastline	Willis & Babcock, 2000; Zintzen et al., 2011, 2012
	Poor Knights Islands	Denny et al., 2004
	Tawharanui MPA	Willis et al. 2003
Philippines	Panglao Region – Bohol Sea	Barord et al., 2014

Table II (continued): Examples of the use of BRUVS in MPAs and other areas of ecological interest around the world.

Country	Location	Reference
Réunion Island (France)	Saint-Paul Bay	Loiseau et al., 2016
Spain	Columbretes Islands Marine Reserve	Stobart et al., 2015
	Western Mediterranean	Stobart et al., 2007
Taiwan	Third Nuclear Power Plant (southern region)	Jan et al., 2007
United States of America	Gulf of Mexico	Gledhill et al., 2005; Reynolds et al., 2018